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Transposable elements in sexual and asexual animals

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Wahrlich es ist nicht das Wissen, sondern das Lernen,
nicht das Besitzen, sondern das Erwerben,
nicht das Da-Seyn, sondern das Hinkommen,
was den grössten Genuss gewährt.

– *Schreiben Gauss an Wolfgang Bolyai, 1808*

Curriculum Vitae

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NAME	Jens Bast
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Education

2011-2015	PhD thesis (biology) *Georg-August University Goettingen* Title: 'Transposable elements in sexual and asexual animals'
2003-2010	Study of biology, diploma *University of Technology Darmstadt* Specialization in Ecology, Evolution and Genetics
2002	Abitur (A-Levels) *Alfred-Grosser Gymnasium Bad Bergzabern*

Teaching

2014	Workshop for ecological and evolutionary methods at the service of plant protection (NGS – a fast forward guide & metagenome data handling) *Nanjing Agricultural University*
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2012	MSc practical course functional soil ecology *Georg-August University Goettingen*
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Conference Contributions

2011-2014 GOEvol Network & Symposium on Evolutionary Biology
Georg-August University Goettingen
Foundation member of GOEvol (in 2011); organization and hosting of annual conferences and workshops

2014 SMBE 2014
San Juan
Chair and organization of session: Genome evolution and adaptation in asexual lineages

2014 Invited Seminar
Max Planck Institute for Evolutionary Biology Ploen
Talk: Patterns of long-term asexuality in oribatid mites

2014 Invited Workshop: Genomics of Asexual Animals
University of Lausanne
Talk: Patterns of ancient asexuality in oribatid mite genomes

2013 EMBL Symposium: New model systems for linking ecology and evolution
EMBL Heidelberg
Poster: 'Selfish genes in ancient mites'

2013 DZG graduate meeting on evolutionary biology
Georg-August University Goettingen
Chair and organization committee

2013 Invited Seminar
GEOMAR Kiel
Talk: 'Oribatid mites as models for long-term maintenance of asexuality'

2012 Genomic impact of eukaryotic transposable elements
Asilomar
Talk: 'Comparing TE load in sexual and asexual oribatid mite lineages using whole genome information'

2011 13th congress of the ESEB
Tuebingen
Talk: Transposable elements in sexual and asexual mites

Internships

2013 Summer School: Advancing tools for biodiversity studies: Genomics and bioinformatics of cnidarians with a focus on corals
Hawaii Institute of Marine Biology

2012 Workshop on genomics; Advanced topic session: BioPython
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Publication List

Peer-reviewed articles

2014 *Science* 344 738-742

Soria-Carrasco V, Gompert Z, Comeault AA,Farkas TE, Parchman TL, Johnson JS, Buerkle CA, Feder JL, ***Bast J****, Schwander T, Egan SP, Crespi BJ, Nosil P*

Stick insect genomes reveal natural selection's role in parallel speciation

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Genomic evidence for ameiotic evolution in the bdelloid rotifer *Adineta vaga*

2012 *Mobile Genetic elements* 2:5 253-256

Kraaijeveld K and ***Bast J***

Transposable element proliferation as a possible side effect of endosymbiont manipulations

Book Contributions

2012 Book chapter

Kraaijeveld K and ***Bast J***

The genomic consequences of asexual reproduction.
In: de Sousa F and Munévar G (Eds.); Sex, Reproduction and Darwinism. London, Pickering and Chatto

Articles emerging from this thesis

In prep *Bast J, Schaefer I, Maraun M, Scheu S and Kraaijeveld K*

Transposable elements in animals of varying age and reproductive mode

In prep *Bast J, Brandt A, Geyrhofer L, Flot JF and Scheu S*

A simple **s**ingle-copy gene **c**overage **roo**ted **g**enome-size **e**stimation method (SCROOGE)

Articles in preparation

In prep *Brandt A, Bast J, Schaefer I and Scheu S*

No mutation accumulation in asexual oribatid mites

In prep *Bast J, Brandt A, Schaefer I, Scheu S, Schwander T, Flot JF and Kraaijeveld K*

The genome of the automictic oribatid mite *Platynothrus peltifer*

In prep *Kraaijeveld K, Anvar Y, Frank J, Bast J, Geuverink E, Wilbrandt J, Petersen M, Ziesmann T, De Knijff P, Ellers, J and Den Dunnen J*

The genomic signatures of *Wolbacha*-induced parthenogenesis in a parasitoid wasp

In prep *Bast J, Dahl M and Flot JF*

Mitochondrial genome regulation by long-noncoding RNAs

In prep *Wei Z, Hu J, Jousset A, Gu Y, Yang T, Bast J, Shen Q, Yin S and Xu Y*

Pathogen invasion disrupts host rhizosphere microbiome

CONTENTS

SUMMARY

The prevalence of sexual reproduction among eukaryotes despite its marked disadvantages is one of the most elusive problems in evolutionary biology. The observation that most asexual eukaryotes are recent offshoots scattered throughout the eukaryotic tree of life has led to the common assumption that asexual species are bound for early extinction. Numerous ecological and genetic models seek to explain this pattern. One prominent set of models predict that mutation accumulation leads to the extinction of asexual lineages. Even so, for mutation accumulation to outweigh the cost of sex, these models require unrealistically high mutation rates. Potentially however, transposable elements (TEs) pose a threat for newly arisen asexual lineages. Transposable elements are replicating independently from the host's cell cycle and can induce deleterious effects on the host. Theory predicts that upon the switch to asexuality, TEs should accumulate because of inefficient purifying selection, potentially driving the lineage to extinction. However, interests of hosts and TEs should align in asexuals, leading to the evolution of less harmful TE dynamics over time.

This thesis investigated these predictions by identifying TEs in a range of animal species with different lineage age and reproductive mode using complete genome data. Overall, there was no evidence for TE accumulation in independent lineages that recently switched to asexuality (*Leptopilina* and *Daphnia*). However, certain TE families (*Gypsy*) were more abundant in asexuals, which might reflect the early stages of TE increase in these asexual taxa. By contrast, species under prolonged asexuality, i.e. the apomictic bdelloid rotifer *Adineta vaga* and automictic oribatid mites, harbored only few and mostly inactive TEs. The purge of TEs from populations over time might require certain prerequisites, such as large population size and effective host defence. Moreover, this thesis argues that TE dynamics in recently arisen asexual lineages are also affected by the mechanism through which the transition to asexuality is achieved.

The results of this thesis suggest that the early extinction of asexual populations is unlikely to be caused by an overall expansion of TE copies in their genomes, but potentially by certain TE types if not contained. Furthermore, TEs might be cleared from asexual species over time in at least some cases.

Zusammenfassung

Die Dominanz von sexueller Reproduktion im Reich der Eukaryoten trotz deutlicher Nachteile ist eines der schwierigsten Probleme der Evolutionsbiologie. Die Beobachtung, dass die meisten asexuellen Eukaryoten rezente und verstreute Linien des Stammbaums des Lebens sind, hat zu der verbreiteten Annahme geführt, dass asexuelle Arten schnell aussterben. Zahlreiche ökologische und genetische Modelle versuchen dieses Muster zu erklären. Ein vorherrschendes Modell sagt vorraus, dass das Aussterben von asexuellen Linien mit der Anhäufung von Mutationen einhergeht. Allerdings müssen diese Modelle unwahrscheinlich hohe Mutationsraten annehmen, um die Nachteile von sexueller Reproduktion aufzuwiegen. Möglicherweise könnten jedoch Transposable Elemente (TEs) eine Bedrohung für neu entstandenene asexuelle Linien darstellen. Transposable Elemente replizieren sich unabhängig vom Wirtszellzykus und können schädliche Auswirkungen auf das Wirtsgenom haben. Theoretisch könnten TEs durch ineffiziente negative Selektion in neuen asexuellen Linien akkumulieren und zu deren Aussterben führen. Allerdings sollten sich mit der Zeit die Interessen von Wirt und TEs angleichen, was zu Evolution weniger schädlichen TEs führen sollte.

Die vorliegende Arbeit untersuchte diese Hypothesen mittels Komplettgenomdaten um TEs in verschiedenen Tierarten mit unterschiedlichem Linienalter und Reproduktionsmodus zu identifizieren. Insgesamt konnte nicht nachgewiesen werden, dass TEs in unabhängigen rezenten asexuellen Linien (*Leptopilina* und *Daphnia*) akkumulieren. Allerdings waren bestimmte TE Familien (*Gypsy*) in den Asexuellen häufiger, was das Frühstadium von TE Anhäufung in diesen Taxa darstellen könnte. Demgegenüber beinhalteten Arten, die schon länger asexuell sind, i.e. die apomiktische Bdelloide *Adineta vaga* und automiktische Hornmilben, nur wenige und größtenteils inaktive TEs. Die Eliminierung von TEs von Populationen mit der Zeit könnte bestimmte Vorraussetzungen, wie hohe Populationsgrößen und effektive genomische Verteidigungsmechanismen benötigen. Außerdem argumentiert diese Arbeit, dass TE Dynamiken in rezent entstandenen asexuellen Linien auch von dem Mechanismus des Übergangs von Sexualität zur Asexualität beeinflusst werden.

Die Ergebnisse dieser Arbeit deuten darauf hin, dass eine allgemeine Ausbreitung von TE Kopien in Genomen nicht für das vorzeitige Aussterben von asexuellen Populationen verantwortlich ist, sondern eher bestimmte TE Typen, wenn diese nicht vom Wirtsgenom kontrolliert werden können. Des Weiteren können TEs von asexuellen Arten zumindest in manchen Fällen mit der Zeit eliminiert werde.

Contributions to the chapters of this thesis

Chapter 2

Genomic evidence for ameiotic evolution in the bdelloid rotifer *Adineta vaga*

Contributions to transposable element detection and identification; general discussions of major findings with main authors and contributions to the figures and text

Chapter 3

Transposable element proliferation as possible side effect of endosymbiont manipulations

Contributions to the general idea; generation of figures; contributions to writing of text

Chapter 4

Transposable elements in animals of varying age and reproductive mode

General design of the study; complete execution of methodology; writing of text and generation of figures

I | General Introduction

1.1 Many ways to be asexual

Nature provides various ways to reproduce, and a large variety to do this asexually (Bell 1982; Schön *et al.* 2009; Kraaijeveld & Bast 2012; Schwander *et al.* 2014). Cyclical parthenogens alternate sexual and asexual cycles, depending for example on the scarcity of resources or other environmental conditions. Selfing hermaphrodites go through both egg and sperm production and fuse gametes within the same individual to produce offspring. Other parthenogenetic animals need to be stimulated by sperm for the development of eggs, but the sperm then does not contribute to the genome of the offspring. In haplodiploid (arrhenotokous) hymenopterans, males are produced clonaly from unfertilized eggs, females from fertilized eggs. Haplodiploid systems may become completely thelytokous through *Wolbachia* endosymbionts. One peculiar example of asexuality occurs in the red fire ant (*Wasmannia auropunctata*). In these colonies, males are clonal and share no genes with female queens, which are also clonal (Fournier *et al.* 2005). Male genes are not passed on to the next generation. These are examples of the range of asexual lifestyles (Bell 1982).

1.2 The advantages of sex

Despite different strategies for an asexual lifestyle and a demographic 'two-fold' advantage over sexual reproduction, that comes with omitting males, asexual lineages are scarce (1% of eukaryotic taxa) and mostly isolated branches within sexual clusters scattered throughout the eukaryotic tree of life (Maynard Smith 1978; Bell 1982; Butlin 2002; Schön *et al.* 2009). This 'twiggy' distribution is commonly interpreted as young lineage age. With the overwhelming majority of eukaryotes reproducing sexually, sex must have some major advantage overcoming its costs of producing males and splitting up favorable allele combinations (Weismann 1889; Maynard Smith 1978).

Over twenty genetically- and ecologically-centered theories seek to explain why asexual lineages are doomed to early extinction compared to sexual lineages and why sex is favorable despite its costs (Kondrashov 1993; West *et al.* 1999). Genetic models explain the

demise of asexuals through the accumulation of deleterious mutations, caused by linkage to advantageous alleles resulting in reduced efficacy of natural selection together with the loss of least-loaded genotypes (mutational meltdown) and the inability to combine beneficial mutations in a single individual [Muller's ratchet (Muller 1932, 1964), Kondrashov's hatchet (Kondrashov 1988), Hill-Robertson (Hill & Robertson 1966; Felsenstein 1974), Fisher-Muller-accelerated-evolution (Fisher 1930)]. Ecological models are based on species-environment interactions and propose that strong biotic interactions or spatially variable niches drive sexual reproduction by favoring diverse genotypes [e.g., Red Queen hypothesis (Jaenike 1978; Hamilton 1980), Tangled Bank hypothesis (Ghiselin 1974; Bell 1982)]. However, multiple mechanisms might not be mutually exclusive but act at the same time, or different mechanisms may act in different populations or environments (West *et al.* 1999). For example, mutational meltdown does not explain the proximate cause for the occurrence of asexual lineages in certain habitats, as it does not provide a sufficient advantage for sex in the short-term (Williams 1975; Maynard Smith 1978; Bell 1982). But mutational meltdown might be what drives some species to extinction over time. A pluralist approach, like the Structured Resource Theory of Sexual Reproduction (SRTS), explains the benefit of sex with optimal exploitation of slowly regrowing, complex resources in limited supply by generating diverse genotypes depending on environmental fluctuations (Scheu & Drossel 2007; Song *et al.* 2011, 2012).

1.3 Model organisms for testing theories of sexual and asexual evolution

Testing theories needs suitable model systems. Disentangling the effects of reproductive mode from species-specific effects, such as different life-history traits, population sizes or strength of selection is challenging, but necessary to identify consequences related directly to the mode of reproduction (Neiman & Schwander 2011; Glémin & Galtier 2012). Ideally, model systems should include evolutionary replicates of sexual and asexual populations of different age, that allow comparison of ecologically similar or independent lineages. Further, models that differ in meiotic or mitotic cytology, and thus in their genome linkage and heterozygosity, and that differ in the within-lineage diversity of asexual clusters may help to understand why sex is favored in natural populations (Neiman & Schwander 2011). Also,

models allowing the return to sexuality (e.g., by curing *Wolbachia* infections of haplodiploids) are helpful. Additionally, understanding the advantages of sexual reproduction might come from insights into evolutionary successful asexual species that have been persisting over prolonged time [e.g., bdelloid rotifers and several species of oribatid mites] (Judson & Normark 1996; Butlin 2002; Neiman *et al.* 2009). By using the advantages of different model systems, genetic and ecological strategies that are responsible for the maintenance of sexual reproduction may be identified.

1.4 The Janus-faced nature of TEs

Transposable elements (TEs) are one genomic burden that might be responsible for the demise of asexuals. Transposable elements are short (0.5 – 20 kb) genomic entities found in high abundances in virtually all living organisms (Aziz *et al.* 2010; Hua-Van *et al.* 2011). Their evolutionary success is due to the ability of self-replication and proliferation within the host's soma and germline independent from the host cell cycle, and vertical and horizontal spread throughout populations (Burt & Trivers 2006; Jurka & Kapitonov 2007; Wicker *et al.* 2007; Schaack *et al.* 2010b; Hua-Van *et al.* 2011). In this 'selfish' way, TEs introduce genomic conflict by spreading at the expense of the host's genes (Hickey 1982; Kidwell & Lisch 2001; Burt & Trivers 2006; Werren 2011). Transposition of TEs within genomes is deleterious for several reasons (Nuzhdin & Petrov 2003; Dolgin & Charlesworth 2008; Hollister & Gaut 2009; Blumenstiel 2011; Ågren 2014): random insertions near or into genes disrupt gene functions, ectopic recombinations between TE sequences cause non-homologous chromosomal exchange, and metabolic costs of TE expression are harmful effects to the host. Host genomes can counter TE activity by the establishment of epigenetic silencing. The resulting dynamics of TEs and their counter-actors resemble host-parasite co-evolutionary dynamics (Slotkin & Martienssen 2007; Malone & Hannon 2009; Agren & Wright 2011). On the other hand, TEs potentially promote evolutionary innovations by genetic rearrangements and duplications of the host genome, generating new gene copies and new regulatory units, or by restructuring regulatory networks (Biémont & Vieira 2006; Feschotte 2008; Oliver & Greene 2009, 2012; Werren 2011; Chénais *et al.* 2012; Abrusán *et al.* 2013; Ellison & Bachtrog 2013). However, beneficial effects rather are side-

effects due to the stochasticity of element dynamics, and because there is no selective force to maintain elements in the long-term (Burt & Trivers 2006; Werren 2011).

1.5 TE dynamics in asexual populations

Transposable element dynamics presumably are influenced by the host's reproductive mode (**Fig. 1**) (Hickey 1982; Hua-Van *et al.* 2011; Crespi & Schwander 2012). Sexual reproduction promotes both the spread and elimination of TEs through mixis. Elements expand through populations quickly, thereby resembling sexually transmitted disease (STD) dynamics. However, with mixis purifying selection is more effective and affected alleles may get restored. Furthermore, sexuals are expected to quickly evolve repressors against novel TEs. On the other hand, reduced effective purifying selection through the non-random association of alleles (linkage disequilibrium) in asexuals is predicted to result in accumulation of TEs, possibly leading to the early demise of these lineages through mutational meltdown (Nuzhdin & Petrov 2003; Arkhipova & Meselson 2005). However, the fates of TEs and hosts are coupled in asexuals, and TEs should evolve to be less harmful over time, otherwise elements go extinct with their hosts (Charlesworth & Langley 1986; Wright & Schoen 1999; Nuzhdin & Petrov 2003). This leads to the prediction that recently arisen asexual lineages might experience unchecked proliferation of TEs, whereas old asexual lineages should have a greatly reduced, non-active TE content compared to sexual lineages in order to minimize the mutational burden (Arkhipova & Meselson 2000; Wright & Finnegan 2001; Normark *et al.* 2003). Theoretical simulations support these predictions, with population size being the most critical factor (Dolgin & Charlesworth 2006).

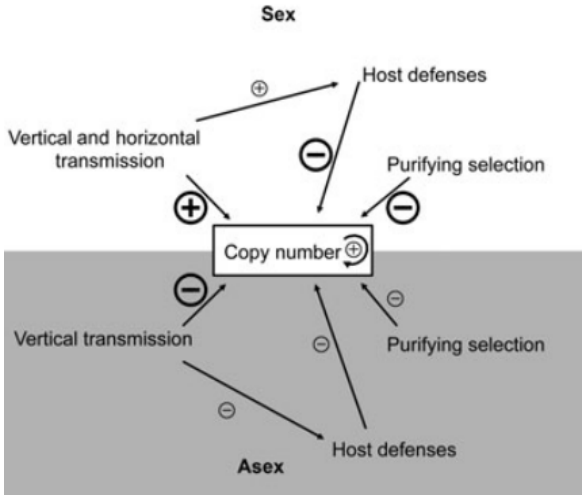

Figure 1: Factors influencing TE load in sexual and asexual lineages from Crespi & Schwander (2012).

Overall, predicting TE load and dynamics is challenging due to the double-edged nature of the interaction between sex and TEs and the manifold factors influencing it. The study of the relationship between TE dynamics and reproductive mode requires suitable model systems, i.e. eligibility to compare lineages of different phylogenetic age and relatedness within the same animal group (see above).

1.6 Model organisms studied in this thesis

Disentangling the effects of reproductive mode on TE dynamics needs the comparison of sexual and parthenogenetic lineages of different age. *Daphnia pulex* (Crustacea, Branchiopoda) lineages used here are younger than 1,000 years, asexual *Leptopilina clavipes* (Insecta, Hymenoptera) lineages are 12,000-43,000 generations old, the bdelloid rotifer *Adineta vaga* (Rotifera, Bdelloidea) is 40 million years (my) old and some oribatid mites putatively are as old as 100 my (Heethoff *et al.* 2007; Kraaijeveld *et al.* 2011; Fontaneto *et al.* 2012; Tucker & Ackerman 2013). This combination of species allows to investigate the consequences of reproductive mode on transposable element dynamics.

The pond-living microcrustacean *Daphnia pulex* is a cyclical parthenogenetic species (hereafter called 'sexual'), within which several obligate apomictic ('asexual') lineages emerged across North America. The transition to asexuality was promoted by meiosis-suppressing genetic elements introgressed into the population by *Daphnia pulicaria* males (Lynch *et al.* 2008). Asexual *Daphnia* lineages seem to suffer mutational meltdown through the exposure of recessive deleterious alleles (Tucker & Ackerman 2013). Previous studies on DNA transposons and LTR elements in *Daphnia* did not reveal clear patterns of TE accumulation for sexual or asexual lineages (Rho *et al.* 2010; Schaack *et al.* 2010a, c).

The parasitoid wasp *Leptopilina clavipes* occurs as haplodiploid sexual and diploid apomictic populations. Asexuals in Northern Europe are derived from a Spanish population infected with parthenogenesis-inducing *Wolbachia* bacteria (Kraaijeveld *et al.* 2011). A first genome-wide TE survey found no evidence for overall increase in TE number in an asexual compared to a sexual lineage (Kraaijeveld *et al.* 2012).

Probably, the most famous and intensely studied asexual group for which males never have been found are bdelloid rotifers (Mark Welch & Meselson 2000; Danchin *et al.* 2011). The bdelloid group comprises more than 460 species (Segers 2007). Organisms live in freshwater and semi-terrestrial habitats like mosses and lichens and temporary ponds. Bdelloids reproduce via apomixis and thus without meiosis. Fossils in amber are older than 40 million years, but the whole group might be as old as 80 my (Fontaneto *et al.* 2012). They are able to withstand high amounts of radiation using extremely efficient DNA repair and endure desiccation by going through an anhydrobiosis state (Gladyshev & Meselson 2008; Hespeels *et al.* 2014). The dried propagules allow to rid lethal fungal parasites and promote dispersal (Wilson & Sherman 2010). Bdelloids can reach a high local diversity, have a widespread distribution and are able to radiate and adapt in the absence of sex (Fontaneto *et al.* 2008, 2012). Consistent with mutational accumulation theory, genomes contain very few TEs, which are mostly decayed or recent arrivals (Arkhipova & Meselson 2000; Gladyshev *et al.* 2007; Gladyshev & Arkhipova 2010). A particular feature of bdelloid rotifers is the ability to incorporate genes by horizontal transfer from bacteria, fungi and plants into their genomes (Gladyshev *et al.* 2008).

One other model system for elucidating the evolution of sex comes from soil-living animals, where asexuals are frequent, wide-spread and often co-exist with closely related ecologically similar sexual taxa (Bell 1982; Maraun *et al.* 2012). The tiny ($<$ 1 mm) oribatid mites (Acariformes, Oribatida) are the animal group comprising most eukaryotic parthenogenetic species (10% of the group), are species-rich ($>$ 10,000 species) and highly abundant (up to 350,000 ind./m^2) (Maraun & Scheu 2000; Heethoff *et al.* 2009; Maraun *et al.* 2012). Several families are exclusively parthenogenetic (Norton & Palmer 1991; Norton *et al.* 1993). Parthenogenesis has been a successful strategy for many oribatid mite species as many parthenogenetic lineages are species-rich and evolved and radiated over long periods of time (Maraun *et al.* 2003, 2004; Heethoff *et al.* 2007; Laumann *et al.* 2007; Schaefer *et al.* 2010). These taxa reproduce via thelytoky with terminal fusion automixis (Taberly 1987a, b), potentially with an inverted sequence of meiosis (Taberly 1987a, b; Heethoff *et al.* 2009). Oribatid mites are obligate parthenogens and geographic parthenogenesis has not been described for this animal group.

Fossils of oribatid mites are known since the Devonian (~390 mya; (Norton *et al.* 1988)), but molecular data suggest that oribatid mites likely were among the earliest colonizers of land and originated in the Cambrian to Precambrian era (571 ± 37 mya; Schaefer *et al.* 2010). Sex determination mechanisms are unknown and diploid chromosome number is mostly 18 (Heethoff *et al.* 2006, 2009).

All model organisms have benefits but also caveats, specifically when investigating organisms from natural populations. The most important point is presence of evolutionary replicates of different phylogenetic relatedness and age. Comparing the organisms studied in this thesis, oribatid mites are the most suitable models regarding this kind of replicates. Oribatid mites comprise congeneric sexual and asexual groups and whole clades of solely asexual taxa. The occurrence of young, old and ancient lineages and the availability of extensive ecological data renders oribatid mites one of the best suited animal group for investigating mechanisms for the maintenance of sexual reproduction. The *Daphnia* group comprises several sister-populations and taxa, but are very recent parthenogens. Sexual and asexual *Leptopilina* populations are restricted to only one sister pair of young age. However, the possibility to restore sexuality by curing the lineage of *Wolbachia* allows experimental manipulation and introgression. Generally, it is favorable for genome scale investigations and experimental manipulation to culture animals. *Daphnia* and *Leptopilina* can be reared easily, whereas oribatid mites have to be collected in the field and only yield a low amount of DNA. However, with the fast advances of sequencing technology, even these animals can be raised to the state of model-organisms for evolutionary investigations.

1.7 Advances in -omics for ecologists

With the fast advance of technology for generating whole genome sequence data, biologists are experiencing a shift in scale of investigating systems. It is now possible to address questions that were out of reach for non-model organisms just five years ago. The possibility to integrate genomic, transcriptomic, epigenomic, up to population genomic data into evolutionary investigations will have great impact on understanding evolutionary-ecological dynamics. The focus of genetic research can now be expanded from model-

organisms to a large variety of non-model organisms and field studies.

However, there are still caveats when dealing with peculiarities of non-model organisms. Creativity in the application and combination of methods is necessary for organisms with unusual genome structure, high heterozygosity, and - maybe most important for not yet established models - the impossibility of lab-cultures or inbred and isofemale lines. Still most of available lab-wet and computational pipelines are designed for standard model organisms (e.g., fruit fly, mouse, human). However, non-model organisms of ecological and evolutionary importance deviate from most standard approaches because of their different traits and history. Bioinformatic analyses have to be adjusted as well as the biologists way of thinking when confronted with massive amounts of data to handle.

1.8 Outline of this thesis

This thesis investigates the impact of transposable elements on sexual compared to asexual genome evolution. Their role as deleterious factors in genomes is analyzed by comparing their abundance and activity in organisms of different reproductive modes and phylogenetic age using whole genome data. The **main hypothesis**, in concordance with the mutation accumulation theory, is that newly arisen asexual lineages contain a higher TE load compared to sexual sister populations. Oppositely, species under prolonged asexuality should harbor a reduced, inactive TE content to survive over time.

To investigate this hypothesis, I analyzed the TE content of an ameiotic bdelloid rotifer (**Chapter 2**), discussed possible lineage-effects responsible for TE activity (**Chapter 3**) and conducted a study of TE content in sexual and asexual populations of different organisms and age (**Chapter 4**). More specifically:

Chapter 2 is a genomic summary of the bdelloid rotifer *Adineta vaga*, revealing a chromosome structure that is incompatible with conventional meiosis, extensive gene conversion as a counter force to mutation accumulation and low abundances and activity of TEs, all in concordance with predictions of long-term asexual genome evolution. However, these findings might be peculiarities of an 'open genome', with extensive horizontal gene transfer possibly to a degree resembling mixis.

Chapter 3 discusses possible side-effects of *Wolbachia* endosymbionts leading to increased TE abundance in asexual *Leptopilina* wasps by manipulating epigenetic silencing mechanisms. This shows that many factors might be directly and indirectly influencing TE activity in different animal lineages.

Chapter 4 focuses on the fate of TEs as potential mutational factors in sexual and asexual species of varying age. Predicted patterns of TE accumulation are overall not confirmed by comparing *Daphnia*, *Leptopilina* and several oribatid mite lineages. However, some TEs, especially *Gypsy* elements might pose a threat. Even so, asexual lineages are able to maintain low TE load, given large populations and effective control.

The thesis argues that it is most important to combine both ecology and genetics into research investigations to solve the 'queen of problems in evolutionary biology' by searching answers in several suitable model organisms.

II | Research Chapters

Chapter 2 | Genomic evidence for ameiotic evolution in the bdelloid rotifer Adineta vaga

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Loss of sexual reproduction is considered an evolutionary dead end for metazoans, but bdelloid rotifers challenge this view as they appear to have persisted asexually for millions of years (Danchin *et al.* 2011). Neither male sex organs nor meiosis have ever been observed in these microscopic animals: oocytes are formed through mitotic divisions, with no reduction of chromosome number and no indication of chromosome pairing (Hsu 1956). However, current evidence does not exclude that they may engage in sex on rare, cryptic occasions. Here we report the genome of a bdelloid rotifer, *Adineta vaga* (Davis, 1873) (Davis 1873), and show that its structure is incompatible with conventional meiosis. At gene scale, the genome of *A. vaga* is tetraploid and comprises both anciently duplicated segments and less divergent allelic regions. However, in contrast to sexual species, the allelic regions are rearranged and sometimes even found on the same chromosome. Such structure does not allow meiotic pairing; instead, we find abundant evidence of gene conversion, which may limit the accumulation of deleterious mutations in the absence of meiosis. Gene families involved in resistance to oxidation, carbohydrate metabolism and defence against transposons are significantly expanded, which may explain why transposable elements cover only 3% of the assembled sequence. Furthermore, 8% of the genes are likely to be of non-metazoan origin and were probably acquired horizontally. This apparent convergence between bdelloids and prokaryotes sheds new light on the evolutionary significance of sex.

With more than 460 described species (Segers 2007), bdelloid rotifers (Fig. 1) represent the highest metazoan taxonomic rank in which males, hermaphrodites and meiosis are unknown. Such persistence and diversification of an ameiotic clade of animals are in contradiction with the supposed long-term disadvantages of asexuality, making bdelloids an 'evolutionary scandal' (Maynard Smith 1986). Another unusual feature of bdelloid rotifers is their extreme resistance to desiccation at any stage of their life cycle (Ricci 1998), enabling these microscopic animals to dwell in ephemeral freshwater habitats such as mosses, lichens and forest litter; this ability is presumably the source of their extreme resistance to ionizing radiation (Gladyshev & Meselson 2008).

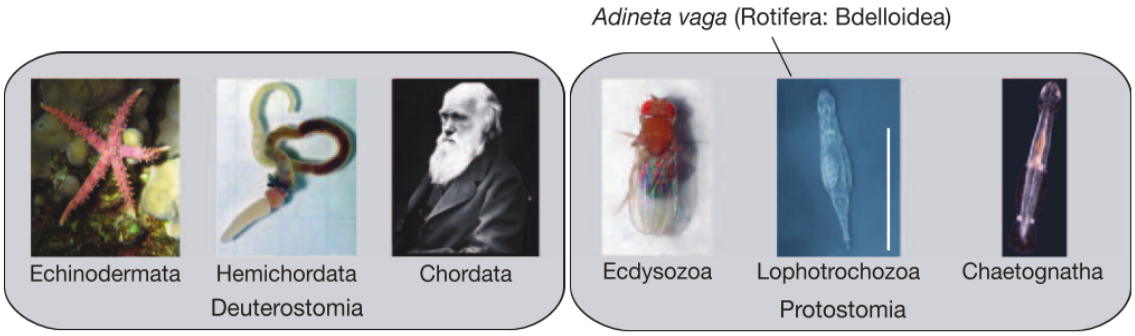

Figure 1: Position of bdelloid rotifers among metazoans. Bdelloid rotifers ('leech-like wheel-bearers') are a clade of microscopic animals (scale bar,100 um) within the phylum Rotifera. Photographs of Hemichordata (*Saccoglossus*), Chordata (*Homo*) and Ecdysozoa (*Drosophila*) courtesy of David Remsen (MBL), John van Wyhe (http://darwin-online.org.uk) andAndré Karwath, respectively.

We assembled the genome of a clonal *A. vaga* lineage into separate haplotypes with a N_{50} of 260 kilobases (kb) (that is, half of the assembly was composed of fragments longer than 260 kb). Assembly size was 218 megabases (Mb) but 26 Mb of the sequence had twice the average sequencing coverage, suggesting that some nearly identical regions were not resolved during assembly (Supplementary Fig. 3); hence, the total genome size is likely to be 244 Mb, which corresponds to the estimate obtained independently using fluorometry (Supplementary Note C2). Annotation of the complete assembly (including all haplotypes) yielded 49,300 genes. Intragenomic sequence comparisons revealed numerous homologous blocks with conserved gene order (colinear regions). For each such block we computed the per-site synonymous divergence (Ks) and a colinearity metric defined as the fraction of colinear genes. Colinear blocks fell into two groups (Fig. 2a): a group characterized by high colinearity and low average synonymous divergence, and a group characterized by lower colinearity and higher synonymous divergence. The presence of two classes of colinear blocks is consistent with a tetraploid structure comprised of alleles (recent homologues) and ohnologues (ancient homologues formed by genome duplication). Allelic pairs of coding sequences are on average 96.2%identical at the nucleotide level (median 5 98.6%) versus 73.6% (median 5 75.1%) for ohnologous pairs. Nearly 40% (84.5 Mb) of the assembled genome sequence is organized in quartets of four homologous regions A_1, A_2, B_1 and B_2, of which A_1-A_2 and B_1-B_2 are two pairs of alleles and As are ohnologous to Bs (Hur *et al.* 2009) (Fig. 2b).

We found evidence of genomic palindromes up to 705 kb in length and involving up to 148 genes. The *A. vaga* genome contains at least 17 such palindromic regions (Fig. 3a) reminiscent of those reported in the Y chromosomes of primates (Rozen *et al.* 2003). In all 17 cases, the arms of the palindromes present the colinearity and divergence signatures of allelic regions and do not have other allelic duplicates in the assembly, suggesting that they arose by inter-allelic rearrangements rather than by local duplications. In addition to these 17 inverted repeats, we observed three direct repeats that present the signatures of allelic blocks and involve up to 50 genes (Fig. 3a). The cumulative length of the assembly fragments (scaffolds) bearing these 20 allelic rearrangements is 7.5 Mb or 3.5% of the genome sequence. Allelic regions that are found on the same chromosome clearly cannot segregate during meiosis. Moreover, we found hundreds of colinearity breakpoints between allelic regions, and the total length of the scaffolds that have no full-length homologue in the assembly due to these breakpoints exceeds 109 Mb or 51% of the genome assembly (including 91 of the 100 largest scaffolds, Fig. 3b and Supplementary Fig. 10). As a result, it is impossible to split the assembled genome of *A. vaga* into haploid sets: the apparent ploidy level of *A. vaga* is scale-dependent, with a tetraploid structure at gene scale versus chromosome-scale haploidy. Such relaxation of constraints on genome structure is reminiscent of other mitotic lineages such as cancer cells (Stephens *et al.* 2011) and somatic tissues (Vijg & Dollé 2002).

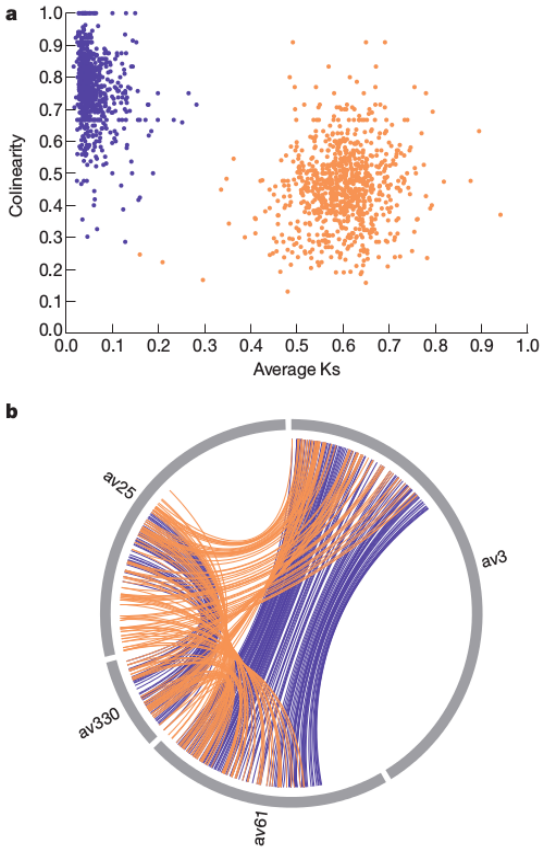

Figure 2: A locally tetraploid genome.

a, Analysis of intragenomic synteny reveals two groups of colinear regions: alleles (in violet, regions characterized by a high fraction of colinear genes and low average Ks, that is, synonymous divergence) and ohnologues (in orange, with lower colinearity but higher Ks). **b**, Example of a genomic quartet of four scaffolds: allelic gene pairs are connected with violet curves and ohnologous gene pairs with orange curves.

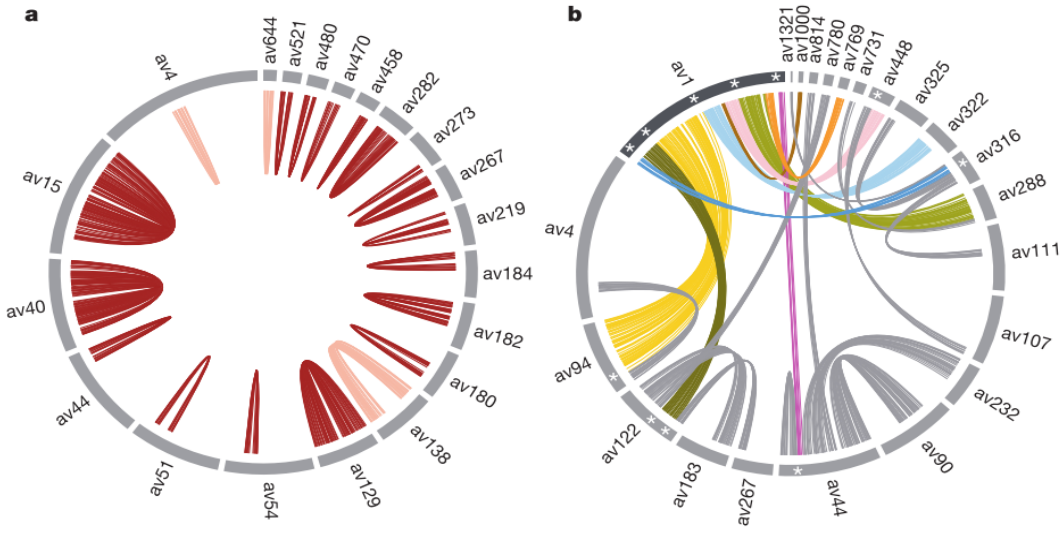

Figure 3: A genome structure incompatible with conventional meiosis. a, In twenty cases, allelic regions are found to occur on the same chromosome. All curves shown connect allelic gene pairs. On three scaffolds both allelic regions have the same orientation (direct repeats, in pink), whereas on the seventeen other scaffolds they are inverted (palindromes, in red). **b**, Local colinearity between alleles does not extend to chromosome scale. Colours are arbitrary and only allelic gene pairs are represented. Asterisks highlight colinearity breakpoints between scaffold av1 and its allelic partners av44, av94, av122, av316 and av448. Further examples for other scaffolds are shown on Supplementary Fig. 10.

It has been proposed that, in the absence of meiosis, alleles accumulate mutations independently from one another, to the point that ancient asexuals may harbour genome-wide allele sequence divergence (ASD) (Birky 1996) larger than inter-individual differences (the so-called 'Meselson effect'). However, the average inter-allelic divergence of *A. vaga* is only 4.4% at the nucleotide level (3% when looking at synonymous divergence), which falls in the upper range reported for sexually reproducing species (Leffler *et al.* 2012). The absence of genome-wide ASD could be explained by low mutation rates and/or by frequent mitotic recombination (such as gene conversion resulting from DNA repair) (Birky 1996). Although there is no evidence of reduced mutation rates in bdelloid rotifers compared with their cyclically sexual sister clade the monogononts (Mark Welch & Meselson 2001), we found strong signatures of recent gene conversion events in the distribution of identity track lengths, that is, distances between consecutive mismatches (Fig. 4a and Supplementary Note E1). We calculated that the probability that a given base in the genome experiences gene conversion is at least one order of magnitude greater than its probability to mutate (Supplementary Note E1), suggesting that homologous regions in the genome of *A. vaga*

undergo concerted evolution (Teshima & Innan 2004). Homogenization through gene conversion may either expose new mutations to selection by making them homozygous or remove them as they get overwritten with the other allelic version (Fig. 4b), thereby slowing Muller's ratchet (that is, their reversible accumulation of detrimental mutations in asexual populations of finite sizes, Supplementary Note E2 and Supplementary Fig. 11).

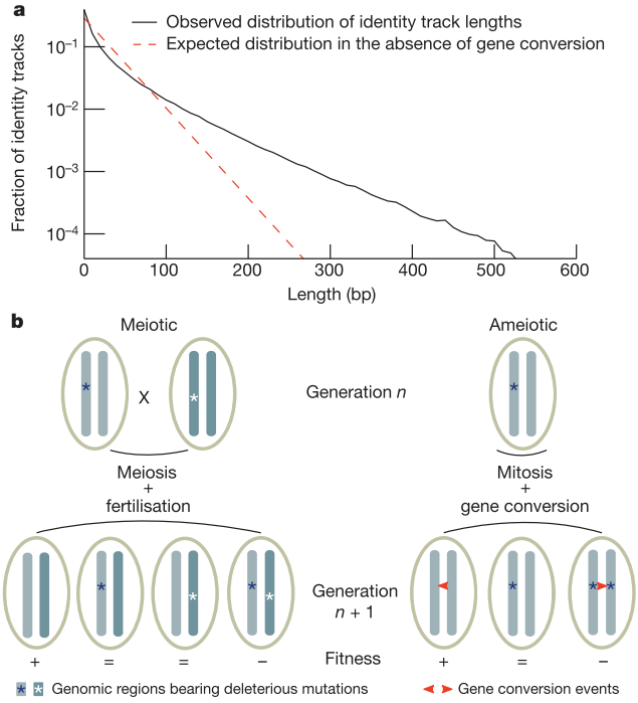

Figure 4: Gene conversion and its evolutionary consequences in ameiotic organisms. a, Evidence for gene conversion between allelic regions. If we suppose that mutations happen at random in a Poisson process of parameter 1/M (where M is the average distance between mutations), then the distance between two consecutive mismatches follows a negative exponential distribution where the proportion of identity tracks of length x equals $e^{-x/M}/M$. Comparison of the observed distribution of identity track lengths with this theoretical distribution reveals a deficit of short tracks and an excess of long tracks, as expected in case of gene conversion. The same pattern was observed when gene-coding regions were excluded from the analysis (data not shown), thereby ruling out a confounding effect of selection. **b**, In sexual organisms, meiotic recombination can generate offspring with fewer or more deleterious mutations (hence increasing or decreasing fitness) than the previous generation. The same outcome is expected in ameiotic organisms that experience gene conversion: a deleterious allele may be overwritten by a beneficial or neutral one, resulting in an increase in fitness, or may overwrite it, resulting in decreased fitness.

Over 8% of the genes of *A. vaga* are much more similar to non-metazoan sequences in GenBank than to metazoan ones (AI log score $>$ 45 (Gladyshev *et al.* 2008), Supplementary Note E4) and were therefore probably acquired through horizontal gene transfer (HGT). This class of genes has significantly fewer introns per kilobase of coding sequence compared with probable core metazoan genes (AI $\geq$ 45, Supplementary Table 2). More than 20% of genes with AI $>$ 45 are found in quartets(groups of four homologous copies in conserved syntenic regions) and were therefore probably incorporated into the rotifer genome before the establishment of tetraploidy, which itself predates the divergence of

extant bdelloid families (Hur *et al.* 2009). The higher the number of copies of a putative HGT gene, the higher its number of introns and the closer its guanine–cytosine (GC) content to the *A. vaga* genome average (Supplementary Fig. 22), which suggests that these parameters reflect the age of acquisition. We also noticed signatures of possibly very recent HGTs: 60 genes with AI > 45 are present in only one copy (with normal coverage), have no intron and have a GC content that is more than 1% above or below the genome average (the same scaffolds also bear genes of probable metazoan origin with AI < 0). In summary, there seems to be an ancient but still ongoing process of HGT at a level comparable to some bacteria (Syvanen 2012).

Some theories predict that transposable elements should be either absent from the genomes of asexuals (Hickey 1982) or undergo unrestrained expansion after the switch to asexuality, potentially leading to species extinction unless transposable element proliferation is prevented (Arkhipova & Meselson 2005). We found that transposable elements cover about 3% of the *A. vaga* genome,which is less than the percentage reported in most other metazoans (including the genome of the obligate parthenogenetic nematode *Meloidogyne incognita*, 36% of which is made up of repetitive elements (Abad *et al.* 2008). Another surprising feature is the high diversity of transposable-element families and the extremely low copy numbers observed for each of them (Supplementary Table 3). Out of 255 families, the overwhelming majority (209) are represented by only one or two full-length copies (for 24 families, no full-length copies could be identified), and for each full-length copy there are, on average, only about ten times as many transposable-element fragments. This relatively low abundance of decayed copies and the fact that long-terminal-repeat (LTR) retro-transposons have identical or nearly identical LTRs (Supplementary Table 4) suggest that most low-copy-number families represent recent arrivals. This is consistent with an ongoing process of acquisition of transposable elements by HGT.

This hypothesis is further supported by the significantly higher density of transposable elements observed around HGTs and vice-versa (Supplementary Note E5). If *A. vaga* has been acquiring transposable elements by HGT, a question that arises is what keeps their number lower than in most other metazoans. Many fragmented copies have apparently been formed through microhomology-mediated deletions. Excision of LTR retrotransposons has

also been occurring through LTR–LTR recombination, leaving behind numerous solo LTRs: for example, two *Juno1* insertions, *Juno1.1* and *Juno1.2*, which were present as full-length copies in the 2006 *A. vaga* fosmid library (Gladyshev *et al.* 2007), exist in the current assembly only as solo LTRs (in the same genomic environments and with the same target site duplications). Finally, there is evidence for expansion and diversification of the RNA-mediated silencing machinery. In addition to Dicer1 proteins, which are shared by all metazoans, *A. vaga* possesses a deep-branching Dicer-like clade with uncertain taxonomic placement (Supplementary Fig. 20). The Argonaute/Piwi and RNA-directed RNA polymerase (RdRP) families are also expanded (Supplementary Figs. 18 and 19). It is plausible that these proteins participate in epigenetic silencing of transposable elements (as was recently observed for single-copy transgenes in *Caenorhabditis elegans* (Shirayama *et al.* 2012), thereby preventing horizontally transferred transposable elements from multiplying upon arrival.

Overall, the genome of *A. vaga* comprises more genes than usually reported for metazoans (Supplementary Note F2), as its haplotypes were assembled separately. Even taking this into account, the gene repertoire of *A. vaga* features expansion of several gene families. For example, the genome of *A. vaga* comprises 284 homeobox superclass genes, mostly found in four copies (quartets) but not organized in clusters; very few ohnologues have been lost, resulting in more homeobox genes than in any other metazoan genome sequenced (Supplementary Note F5). Genes putatively related to oxido-reduction processes are substantially more abundant in *A. vaga* than in other metazoan species, and most of the corresponding genes appear to be constitutively expressed (Supplementary Table 9). This is consistent with the recent report of an effective antioxidant protection system in bdelloid rotifers (Krisko *et al.* 2012). Carbohydrate-active enzymes (CAZymes) in the genome of *A. vaga* are also notably diverse and abundant, with 1,075 genes falling into 202 characterized families. With 623 glycoside hydrolases (involved in the hydrolysis of sugar bonds) and 412 glycosyltransferases (responsible for building sugar bonds), the CAZyme richness of *A. vaga* ranks highest among metazoans and is only comparable to some plants such as poplars (Geisler-Lee *et al.* 2006). *A. vaga* has the richest repertoire of glycoside hydrolases of any organism sequenced so far, hinting at a diversity of feeding habits; 52% of the CAZymes

have an AI > 45 and were therefore probably acquired through horizontal gene transfer.

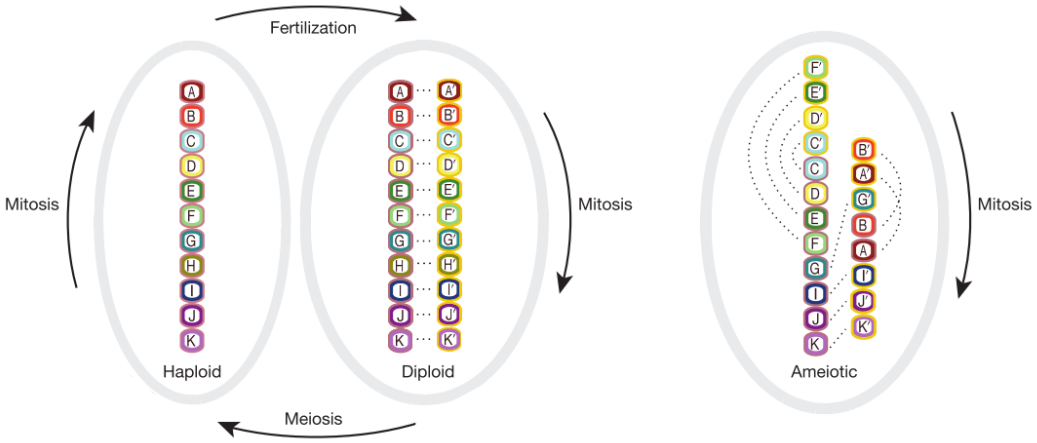

Figure 5: Meiotic versus ameiotic genome structures. Genes are represented with letters,and dashed lines connect allelic gene pairs. A meiotic genome (left) alternates between a haploid phase (in which a single allele of each gene is present) and a diploid phase (in which the genes are present in two allelic versions arranged colinearly on homologous chromosomes). In the ameiotic genome of *A. vaga* (right), alleles are distributed in blocks that are shuffled across chromosomes, resulting notably in intrachromosomal repeats (direct or inverted). As a consequence, chromosomes have no homologues and cannot be paired.

A. vaga has lost 1,250 genes compared with the inferred last common ancestor of Protostomia, the genome of which comprised at least7,844 unique protein-coding genes (Supplementary Note E6). A total of 137 PFAM domains typically present in metazoans could not bedetected in the assembled genome sequence (Supplementary Data 10). Of particular interest are missing domains involved in reproductive processes (Supplementary Note F1); for example, the *Zona pellucida*-like domain (notably found in sperm-binding proteins (Bork & Sander 1992)) is present in an average of 36 copies in metazoan genomes but is absent in *A. vaga*. In contrast, we found multiple copies of most metazoan genes involved in DNA repair and homologous recombination, including a considerably divergent *Spo11* but no *Rad52* and *Msh3*.

To conclude, our analysis of a lineage of the bdelloid rotifer *Adineta vaga* reveals positive evidence for asexual evolution: its genome structure does not allow pairing of homologous chromosomes and therefore seems incompatible with conventional meiosis (Fig. 5). However, we cannot rule out that other forms of recombination occur in bdelloid populations in ways that do not require homologous pairing, such as parasexuality (Forche *et al.* 2008). The

high number of horizontally acquired genes, including some seemingly recent ones, suggests that HGTs may also be occurring from rotifer to rotifer. It is plausible that the repeated cycles of desiccation and rehydration experienced by *A. vaga* in its natural habitats have had a major role in shaping its genome: desiccation presumably causes DNA double-strand breaks, and these breaks that allow integration of horizontally transferred genetic material also promote gene conversion when they are repaired. Hence, the homogenizing and diversifying roles of sex may have been replaced in bdelloids by gene conversion and horizontal gene transfer, in an unexpected convergence of evolutionary strategy with prokaryotes.

Methods summary Genomic DNA was extracted from laboratory cultures of a clonal *A. vaga* lineage and shotgun-sequenced using 454 and Illumina platforms at respective coverage of 25 and 440 times (using both single reads and mate reads from inserts up to 20 kb). The 454 reads were assembled into contigs using MIRA (Chevreux *et al.* 1999); the contigs obtained were corrected using single Illumina reads and linked into scaffolds using paired Illumina reads (Boetzer *et al.* 2011) (Supplementary Table 1). We annotated protein-coding genes by integrating evidence from RNA sequencing, *ab initio* predictions and comparison with UniProt. Most synteny and Ka/Ks (non-synonymous divergence/synonymous divergence) analyses were performed using the package MCScanX (Wang *et al.* 2012) and synteny plots were drawn using Circos (Krzywinski *et al.* 2009) .

Supplementary Information is available in the online version of the paper.

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Author Information The sequencing reads and assembly are available at the Sequence Read Archive (accessions ERP002115 and SRP020364 for DNA, ERP002474 and SRP020358 for cDNA) and at the European Nucleotide Archive (accession CAWI000000000), respectively. The assembly and annotation can be browsed and

downloaded at http://www.genoscope.cns.fr/adineta, whereas the result of the orthology analysis is accessible at http://ioda.univ-provence.fr/. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to O.J. (ojaillon@genoscope.cns.fr or ojaillon@mit.edu), J.F.F. (jean-francois.flot@ds.mpg.de) or K.V.D. (karine.vandoninck@fundp.ac.be).

Chapter 3 | Transposable element proliferation as a possible side effect of endosymbiont manipulations

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Mobile Genetic Elements **2:5** 253-256

The mode of reproduction has been predicted to affect the proliferation of transposable elements (TEs). A population that switches from sexual to asexual reproduction could either accumulate TEs because purifying selection becomes less efficient, or a decrease in TE load because the opportunity for horizontal transmission is reduced. A third possibility is that the mechanism that induces asexual reproduction affects TE dynamics as a side effect. We propose two such mechanisms that might explain recently described patterns of TE abundance in sexual and asexual lineages of the parasitoid wasp *Leptopilina clavipes*. Asexual reproduction in this species is induced by endosymbiotic *Wolbachia* bacteria. In order to achieve parthenogenesis in its host, *Wolbachia* might remove methylation or interfere with Argonaute proteins. Both methylation and Argonaute proteins are known to control TE activity in other species. By interfering with either, *Wolbachia* might therefore secondarily hamper the control of specific TEs.

The relationship between mode of reproduction and transposable element(TE) dynamics has been the topic of considerable debate summarized in (Crespi & Schwander 2012). On the one hand, purifying selection is expected to be less efficient in asexual compared with sexual taxa, leading to an accumulation of TE copies in asexuals. On the other hand, sex allows horizontal transmission of TEs and will facilitate the spread of TEs. Which of these driving factors, if any, will be most important is currently an unresolved question. Recent advances in DNA sequencing technology now allow us to address this question on a genome-wide scale. In a recent paper published in Molecular Ecology, we quantified TE loads in sexual and asexual lineages of the parasitoid wasp *Leptopilina clavipes* (Kraaijeveld *et al.* 2012). Parthenogenesis in this species is induced by endosymbiotic *Wolbachia* bacteria, that are thought to have infected *L. clavipes* several thousand years ago (Kraaijeveld *et al.* 2011). Uninfected lineages reproduce sexually. The results of our study were inconsistent with models that predict increases (Dolgin & Charlesworth 2006) or decreases (Wright & Finnegan 2001)in TE load in asexuals compared with sexuals, regardless of TE type. Instead, we found markedly different patterns between the various types of TEs. Loads of DNA transposons were higher in asexuals, while there was no difference between sexuals and asexuals for LTR and LINE-like TEs, except for one or a few

gypsy-like LTR elements. The reasons for these patterns have already been the subject of some speculation (Crespi & Schwander 2012; Kraaijeveld *et al.* 2012) Here, we elaborate on the possibility that TE dynamics are affected by *Wolbachia*. More precisely, we suggest that in order to induce parthenogenesis, *Wolbachia* has to interfere with host cellular processes, which secondarily also interferes with the control of TE activity. While these suggestions are purely speculative at this moment, we discuss them here because we believe that such processes could be of widespread importance.

We suggest two ways in which *Wolbachia*-induced manipulation of the host reproductive machinery could interfere with the repression of particular TE types. These mechanisms are illustrated in Figures 1 and 2.

First, *Wolbachia* might interfere with the normal functioning of proteins from the Argonaute family (Fig. 1). Argonaute-like proteins are involved in many cellular processes, including cell division and gametogenesis (Thomson & Lin 2009). In order for *Wolbachia* to make unfertilized *L. clavipes* eggs develop as females, it has to ensure that these become diploid. It does so by preventing chromosome segregation at the first mitotic division after meiosis (Pannebakker *et al.* 2004). Thus, in gametes infected by *Wolbachia*, the chromosomes duplicate, condense, but then enter G1 without completing mitosis or cytokinesis. The molecular mechanism through which *Wolbachia* achieves this effect is currently unknown. However, one way for *Wolbachia* to prevent the chromosomes from separating after duplication might be to interfere with Argonaute proteins. In mice for example, mutants defective for a protein from the Argonaute family show arrest during early meiosis (Carmell *et al.* 2007). In addition to their role in cell cycle regulation, Argonaute proteins play an important role in the control of TE activity, through a mechanism known as the ping-pong model (Brennecke *et al.* 2007; Aravin *et al.* 2007). Briefly, Argonaute proteins form a complex with short antisense sequences transcribed from defective TEs. These target full-length TE transcripts (Fig. 1A), which they then degrade, resulting in new short sense TE fragments that can bind to other Argonaute proteins. These in turn target antisense transcripts from the defective TEs, resulting in more antisense bait, and so on. If *Wolbachia* would interfere with the abundance or functioning of Argonaute proteins as suggested above, it would automatically hamper the Argonaute-

driven capturing and degradation of TE mRNA (Fig. 1B). These TE transcripts are then left free to be reverse transcribed into cDNA and pasted back into the genome.

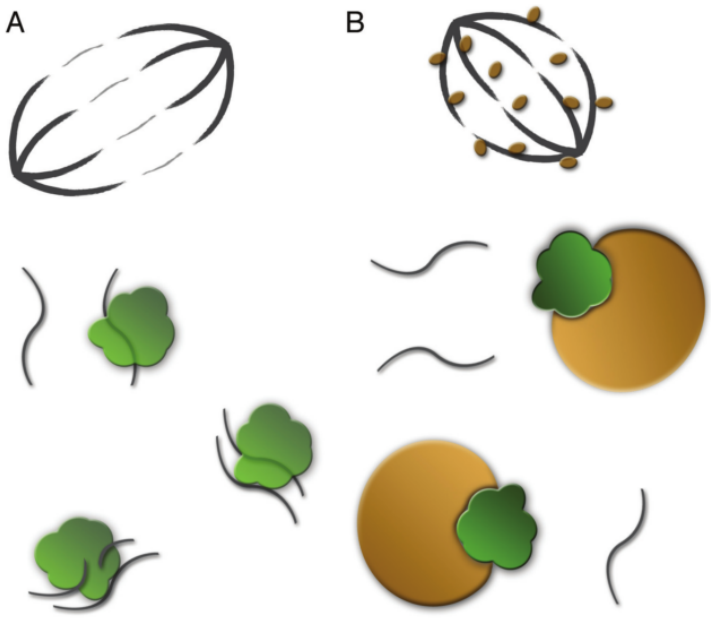

Figure 1: (**A**) Cartoon of a normal dividing cell with meotic/mitotic spindle at the top. Complexes of Argonaute proteins (green) and antisense TE fragments capture and destroy TE mRNAs. (**B**) Dividing cell infected with *Wolbachia*. *Wolbachia* (brown) associate with microtubuli (top) and capture Argonaute proteins (green). TE derived mRNAs are left to insert back into the host genome.

A second way in which *Wolbachia*-induced manipulation of the host could lead to proliferation of TEs is by disturbing normal patterns of DNA methylation. To make unfertilized eggs develop as females, it is not enough for *Wolbachia* to cause diploidization of the gametes as described above. *Wolbachia* also has to prevent diploid zygotes from developing as diploid males. To do so, Wolbachia has to manipulate the host's sex determination mechanism. Several sex determination mechanisms are known in hymenoptera (Sánchez 2008) and it is currently unknown which of these applies to *L. clavipes*. However, since strong inbreeding does not result in diploid males in *L. clavipes* (Kraaijeveld, personal observation), sex determination is unlikely to be based on allelic differences at one or a few genetic loci as in for example the honey bee *Apis melifera*. We therefore assume that sex determination in *L. clavipes* is most likely similar to that described for another parasitoid wasp, *Nasonia vitripennis*. In *Nasonia*, female development requires at least one active copy of the gene *transformer* (*tra*) or a trans-acting factor that

regulates *tra* expression (Verhulst *et al.* 2010). *Tra* is silenced in the female germline, so simple gamete duplication would result in two silenced copies of *tra* and hence male development. In the male germline, however, *tra* is not silenced and males transfer an active copy of *tra* to their offspring. Fertilized offspring therefore inherit both an active and a silenced copy of *tra* and develop as females. To achieve female development of diploidized zygotes, *Wolbachia* has to emulate the male germline and remove silencing of *tra*. The mechanism through which *tra* is silenced is not known, but may involve DNA methylation. If so, Wolbachia could either demethylate the host genome completely, or remove methylation only from *tra*. In the latter case, demethylation could spread to nearby regions of the genome, analogous to the spread of methylation from silenced TEs to nearby genes that has been observed in several species (Kinoshita *et al.* 2007; Martin *et al.* 2009; Rebollo *et al.* 2011).

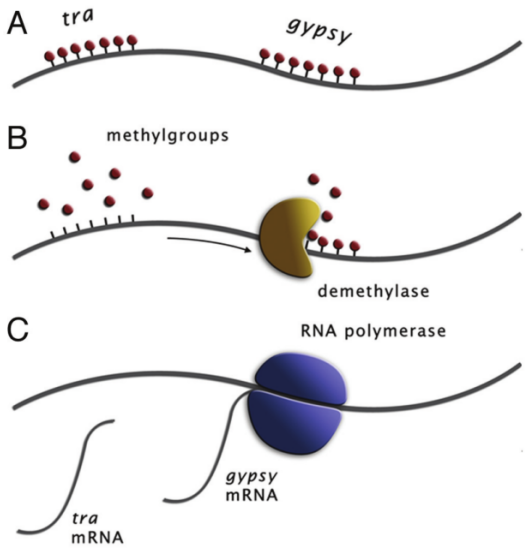

Figure 2: Cartoon of chromosomal region in female germline. (**A**) The sex determination gene *tra* is methylated as well as a nearby *gypsy* element. (**B**) In order to induce female development, *Wolbachia* produces a demethylase that removes methyl groups. (**C**) In the absence of methylation, both *tra* and *gypsy* can be transcribed.

Methylation is a common way of silencing TEs. For example, mutant *Arabidopsis* plants that are defective in their methylation machinery experience bursts of TEs that are normally silent (Tsukahara *et al.* 2009). If Wolbachia removes methylation marks in a non-specific manner to induce female development of the zygote, it may also demethylate nearby TEs, thereby reactivating them (Fig. 2).

Whether either of the above mechanisms actually operates in the *L. clavipes* - *Wolbachia* system is at this stage unknown. We made a start testing the methylation hypothesis by checking for methylation of *gypsy* in sexual and asexual *L. clavipes*. We found that *gypsy* was not methylated in either (Kraaijeveld *et al.* 2012), suggesting that hypothesis 2 cannot account for the high copy number of *gypsy* in asexual *L. clavipes*. We have not tested the

first hypothesis. Our reason for elaborating on the ideas here is because mechanisms like these could play an important role in many systems. Molecular mechanisms that control TE proliferation are often closely related to other important processes. As we point out here, methylation controls the transcription of host genes and TEs. Likewise, the ping-pong model for controlling TEs post-transcriptionally contains components that are important in a wide variety of cellular processes. Other mechanisms that control TEs may similarly have other functions in host cells. It follows that interference of methylation, Argonaute proteins or other mechanisms by endosymbiotic bacteria or other environmental factors would disrupt multiple processes at once, including TE control.

Acknowledgements We thank Bart Pannebakker for helpful comments on an earlier draft of this paper.

Chapter 4 | Transposable elements in animals of varying age and reproductive mode

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In Preparation

The prevalence of sexual reproduction among eukaryotes despite its demographic 'two-fold' cost is a central question in evolutionary biology. Genetic models predict the early demise of parthenogenetic lineages through accumulation of transposable elements (TEs), due to reduced efficiency of purifying selection. However, asexual reproduction should align the interests of hosts and TEs, leading to a decrease in TE abundance and activity given sufficient time. This predicts accumulation of deleterious TEs in newly arisen asexual lineages but a lower TE load in asexual lineages that have persisted for prolonged periods as compared to sexuals. To investigate this hypothesis, we analyzed the TE content of three animal groups (*Daphnia*, *Leptopilina* and oribatid mites) of varying phylogenetic age using whole genome data. For four oribatid mite species we generated draft genomes for *de novo* TE identification. We compared TE abundance using an approach that was particularly robust for cross-species comparisons. We found no overall differences in TE load between lineages of different reproductive modes. The genomes of *Daphnia* and *Leptopilina* harbored recently active TEs. By contrast, both sexual and asexual oribatid mite lineages generally harbored few TEs and showed no signs of recent TE activity. However, specific *Copia* and *Gypsy*-like elements were more frequent in asexual *Daphnia* and *Leptopilina* lineages compared to related sexuals but were rare in asexual oribatid mites. *Gypsy* is a harmful element that is able to spread quickly through populations. The scarcity of such TEs in asexual oribatid mites might indicate that persistence of asexual lineages over long periods of time requires the purging of such TEs from the genome.

Introduction

Transposable elements (TEs) are ubiquitous genomic entities present in virtually all organisms (Aziz *et al.* 2010; Hua-Van *et al.* 2011). Their success relies on the ability to proliferate within and throughout host genomes and populations largely independent of the host's fitness (Hickey 1982). These TE activities occasionally are beneficial to the host, but most insertions are deleterious (Burt & Trivers 2006; Hua-Van *et al.* 2011; Werren 2011). As such, TEs potentially contribute to the 'mutational meltdown' of parthenogenetic lineages (Wright & Schoen 1999; Arkhipova & Meselson 2005). Multiple (counteracting)

forces influence TE accumulation, hence disentangling the effects of reproductive mode on TE dynamics is challenging (Crespi & Schwander 2012). With mixis, sexual reproduction provides a mechanism for both TE spread and limitation of TE accumulation. Elements are able to be transmitted horizontally throughout the host's population, but are purged by purifying selection and countered by an evolutionary response of host defence mechanisms. In parthenogenetic organisms, strong linkage disequilibrium reduces these limiting effects. However, fates of the asexual host and TEs are coupled as elements are restricted to vertical transmission. This leads to the theoretical prediction of increased TE accumulation and activity in newly arisen asexual lineages, as opposed to decreased TE loads and activity in older asexual lineages that went through a 'delayed purge', i.e. after an initial increase, deleterious mutations and TEs are removed over time (Wright & Finnegan 2001; Dolgin & Charlesworth 2006).

Evidence for this hypothesis has been inconclusive due to limitations of methodology and model systems. Previous studies that tested this hypothesis were limited to pairs of single sexual and asexual sister-lineages or single asexual lineages and generated ambiguous patterns of TE dynamics with respect to reproductive mode. *Daphnia pulex* lineages that switched to obligate asexual reproduction less than 1,000 years ago contain fewer TE copies compared to sexual lineages, but studies were confined to specific TE elements (Rho *et al.* 2010; Schaack *et al.* 2010c). Genomes of *Leptopilina clavipes* wasp lineages that became asexual 12,000 – 43,000 generations ago harbor a slightly increased load of DNA transposons and *Gypsy*-like LTR (Long Terminal Repeat) elements (Kraaijeveld *et al.* 2012). However, this study was limited to TEs identified in other organisms, potentially missing many lineage-specific elements. By contrast, the genome of the ameiotic bdelloid rotifer *Adineta vaga* contains diverse TEs, few of which are full-length (Flot *et al.* 2013); chapter 2). In plants, 0.1 million years old (myo) selfing *Capsella rubella* and outcrossing *C. grandiflora* lineages show no difference in TE numbers and dynamics, whereas comparisons of 0.5 myo selfing *Arabidopsis thaliana* and outcrossing *A. lyrata* lineages revealed a higher and more diverse TE content in outcrossing plants (de la Chaux *et al.* 2012; Slotte *et al.* 2013).

To investigate the effect of lineage age on TE dynamics in asexual genomes, we studied TE abundance and activity in whole genome sequencing data of animal taxa with different reproductive modes and lineage age: (1) two sexual and two asexual lineages of *D. pulex* sampled from populations in Ontario and Minnesota (Tucker & Ackerman 2013); (2) sexual and *Wolbachia* infected asexual populations of the parasitoid wasp *L. clavipes (Kraaijeveld et al. in prep*) and (3) two sexual and two asexual species of oribatid mites (asexual *Platynothrus peltifer, Hypochthonius rufulus* and sexual *Steganacarus magnus, Achipteria coleoptrata*).

The pond-living microcrustacean *D. pulex* is a diploid, cyclical parthenogenetic species with several independent apomictic ('asexual') lineages that emerged recently ($<$ 1,000 years ago) across North America. The transition to obligate asexuality was promoted by introgression of meiosis-suppressing genetic elements into the population by *D. pulicaria* males (Lynch *et al.* 2008). The parasitoid wasp *L. clavipes* occurs as haplodiploid arrhenotokous ('sexual') and homozygous diploid thelytokous ('asexual') populations. The transition to asexuality was induced by *Wolbachia* infection of Northern European populations about 12,000-43,000 generations ago i.e., about 6,000 to 21,500 years ago (Kraaijeveld *et al.* 2011). Oribatid mites comprise several parthenogenetic lineages in different phylogenetic groups. Within "Desmonomata", five out of seven and within Enarthronota, 10 out of 13 genera are parthenogenetic. Of these, 80% form exclusively parthenogenetic ('asexual') and species rich clusters (Norton & Palmer 1991; Norton *et al.* 1993; Norton 1998; Maraun *et al.* 2004; Schaefer *et al.* 2010). These diploid taxa reproduce via thelytoky with terminal fusion automixis (Taberly 1987a; b), potentially with an inverted sequence of meiosis resulting in heterozygous lineages (Taberly 1987a; b; Heethoff *et al.* 2009).

Here, we compare TE dynamics of sexual and asexual animals of different reproductive mode and phylogenetic age using standardized methods. We test the prediction that lineages first accumulate TEs upon the switch to asexual reproduction, but loose TEs under prolonged asexuality. Accordingly, we predict that asexual *Daphnia* and *Leptopilina* lineages have a higher TE abundance compared to sexual sister-lineages, whereas asexual oribatid mite species have a diminished TE load compared to sexual species. Likewise, TEs are

predicted to show signs of recent activity in newly arisen, but not older asexual lineages. We estimated (i) overall repeat content, (ii) abundance of lineage-specific TEs and (iii) TE activity throughout evolutionary history.

Material & Methods

For genome-wide TE load comparisons between sexual and asexual lineages, we applied standardized methods designed to control for TE sequence fragmentation and detection bias. We applied the following approach: (i) characterization of overall genomic repetitive content, (ii) calculation of copy numbers for each TE library entry and (iii) inference of TE activity through evolutionary history using repeat landscapes. Draft genome assemblies and repeat libraries were available for *Daphnia* and *Leptopilina.* For oribatid mites we generated draft genome assemblies from pooled populations and identified repeat libraries *de novo.*

Genomic data

Genomic next-generation sequencing read data of two sexual (*eb-1*, *lp8b-6*) and two asexual (*sed-2*, *5w-2*) lineages of *D. pulex* were retrieved from Tucker & Ackerman (2013). The complete *D. pulex* genome was downloaded from NCBI (Acc. no. ACJG00000000.1, (Colbourne *et al.* 2011). The parthenogenetic *L. clavipes* genome and reads from a sexual (*epg*) and an asexual (*gbw*) lineage were obtained from Kraaijeveld et al. (*in prep*). *De novo* sequencing was conducted for four oribatid mite species: the sexual species *Achipteria coleoptrata* (Oribatida, Brachypylina) and *Steganacarus magnus* (Oribatida, Mixonomata) and the asexual species *Hypochthonius rufulus* (Oribatida, Enarthronota) and *Platynothrus peltifer* (Oribatida, Desmonomata). For mite collection, litter and organic soil layer were gathered at the forest of Göttingen. Mites were separated from litter using gradient heat extraction (Kempson *et al.* 1963) and collected in water. Living animals were identified after Weigmann 2006. Prior to DNA extraction, individuals were starved for ten days and cleaned with a brush and by rinsing in water and ethanol. Genomic DNA was extracted from 50 pooled specimens using the DNeasy Blood and Tissue kit (Qiagen; Hilden, Germany) following the manufacturer's protocol. Animals were frozen in liquid nitrogen and crushed with a plastic pestle prior to the addition of proteinase K to facilitate tissue lysis.

Purified DNA was eluted in 50 µL AE buffer. Paired-end Illumina sequencing was done at the Leiden Genome Technology Center (LGTC; Leiden, The Netherlands) with a single insert size of 300 bp. *S. magnus* (Sm) and *P. peltifer* (Pp) were run on one lane of a GaIIx system generating 75 bp paired-end reads. *A. coleoptrata* (Ac) and *H. rufulus* (Hr) were run on one lane of a HiSeq2000 system, producing 100 bp paired-end reads. Raw reads of all lineages were quality filtered and duplicates were removed using TRIMMOMATIC and FASTX-TOOLKIT (Bolger et al. 2014; hannonlab.cshl.edu/fastx_toolkit). Mite genomes were assembled using ABYSS (for Sm and Pp) and PLATANUS (for Ac and Hr) with default parameters (Simpson *et al.* 2009; Kajitani *et al.* 2014).

Genome size estimation

Genome size estimation was done by flow cytometry with an Accuri C6 system (BD Biosciences, Erembodegem, Belgium) following Hare & Johnston (2011). The reference animal for co-staining used was *Drosophila melanogaster* with an estimated genome size of 175 Mb (Animal Genome Size Database). The first quarter (approximately the head) of individual mites were removed from frozen animals (-80°C), transferred into Galbraith buffer (Hare & Johnston 2011) and grinded using a dounce homogenizer. Specimens were filtered through a 20 µm nylon mesh and stained with propidium iodide (50 µg/mL) by incubating at 4°C for 2 h. To compare fluorescence signals, samples and reference were run both separately and together to check for 2C peak signals. The flow cytometry run was stopped after a minimum of 500 counts in the 2C peaks.

Additionally, genome sizes were calculated by a simple single-copy gene coverage rooted genome-size estimation method (SCROOGE; Bast *et al. in prep*). In short, quality trimmed raw reads were mapped to known single copy genes (ribosomal proteins L/S, *RNAPolII*, *hsp80*, *ef1a*). Mapped reads aligning for more than 30 bp were kept and duplicates were excluded. Evenness of coverage was checked and mean coverage extracted with TABLET and SAMTOOLS (Li *et al.* 2009; Milne *et al.* 2010). Haploid genome size (assuming allelic reads are mapped) was calculated using the formula Genome size = number of reads * read length / coverage depth. This method outperformed k-mer based methods for several major animal phyla (Bast *et al. in prep*).

Repetitive content

Methods for *de novo* TE detection depend on databases with entries of known elements and might fail to identify unknown, highly fragmented and ancient TEs. Therefore, to get general insights into genomic repetitive content of each lineage or species, 15mer frequencies in one-fold quality trimmed read data were calculated following (Castoe *et al.* 2011) with P-CLOUDS C10 settings (Gu *et al.* 2008). For mites, as genome sizes vary, the one-fold coverage amount of read data equivalent of *A. coleoptrata* was extracted for each species.

TE libraries and detection

Species-specific repeat libraries were downloaded from RepBase for *D. pulex* and obtained from Kraaijeveld *et al.* (*in prep*) for *Leptopilina*. For oribatid mites, *de novo* repeat detection was done using both assembled data and quality filtered raw reads to balance differences between assemblies, running REPEATMODELER (Smit & Hubley 2011) and TEDNA (with 45-60 million reads per species and the -t option set to 30) (Zytnicki *et al.* 2014) on each of the mite assemblies. Output sequences larger than 500 nt were clustered with 95% identity threshold using UCLUST (Edgar 2010) with the centroid option to join fragments and reduce redundancy. To identify transposable elements in the clustered repeat library, REPCLASS (Feschotte *et al.* 2009) and homology repeat searches were run using REPEATMASKER (Smit *et al.* 1996), TBLASTX and BLASTN against RepBase (Jurka *et al.* 2005) and non-redundant NCBI entries (keywords: retrotransposon, transposase, reverse transcriptase, transposon, transposable element; e-value $>$ 1e-30). Sequences were discarded if all annotation methods regarded library entries as 'unknown'. Ambiguous repetitive elements were double checked for identity with the online version of CENSOR (Kohany *et al.* 2006) against RepBase and kept if there were similarities to translated TE entries. All sequences in the TE libraries were blasted against all NCBI entries to remove sequences with high similarity to non-TE entries. All library TE headers were reformatted to match REPEATMASKER naming standards. Resulting TE libraries contained numbered elements classified to super-family level.

TE load

For specific TE load comparisons between sexual and asexual *Daphnia*, *Leptopilina* lineages and oribatid mite species, we followed the method described in Tenaillon *et al.* (2011). In brief, for every species-specific TE library a unique TE library (UTE) was constructed (Supplementary File Ch4SuppUTEs). This was done by splitting the TE library into 104 bp fragments and mapping these back to the original library after which portions of elements or complete elements were removed, if covered more than once. Subsequently, reads for each lineage were mapped against the respective UTE using SSAHA2 with best hit option and homology of 80% (Ning *et al.* 2001). For each TE entry, total reads aligning for more than 30 bp were kept and RPKM calculated to account for differences in sequence fragment length with
(RPKM_entry = (reads_mapped_entry/((length_entry/1000) * (total_reads/1000000))).
GNUPLOT (Williams *et al.* 2010) was used to plot the k-mer histograms and the differences in RPKM TE abundance between lineages. Custom scripts used are found in the Appendix and Supplementary File Ch4SuppScripts.

TE activity comparisons

To assess transposable element activity through evolutionary history, repeat landscapes were computed by calculating the Kimura-corrected divergence of each TE copy from the consensus. First, TEs in the assemblies were identified using REPEATMASKER with the sensitive option and species-specific TE libraries. Following, the TE divergences were gathered using the script calcDivergenceFromAlign.pl and subsequently plotted with createRepeatLandscape.pl implemented in REPEATMASKER.

Statistics

RPKM values were analyzed using linear models in R (R Team 2013). Significance was determined by sequentially dropping terms from the model (the detailed R script is found in the Appendix and as Supplementary File Ch4SuppR). For *Daphnia* and *Leptopilina*, we also constructed a model that took into account the paired structure of the data by including species-specific TE types as a random effect, using the R library nlme.

Results

De novo *draft genomes and TE libraries of oribatid mites*

Flow cytometric genome size estimates resulted in haploid sizes ranging from 164 to 241 Mb for oribatid mite species (Supplementary Fig. S-Ch4.1; Supplementary Table S-Ch4.1). However, animals have no distinctive 'head' and are of tiny size (< 1 mm), making it difficult to accurately identify 2C peaks, yielding flow cytometry results unreliable. We therefore independently estimated genome size using the SCROOGE pipeline (Bast et al. i*n prep*), which yielded estimates that differed from the flow cytometric estimates by 7% to 26% (Table 1).

Table 1: Genome size estimates for four oribatid mite species and assembly statistics for contigs > 200 bp. Ac: *Achipteria coleoptrata*, Hr: *Hypochthonius rufulus*, Sm: *Steganacarus magnus*, Pp: *Platynothrus peltifer*

	Species	**Ac**	**Hr**	**Sm**	**Pp**
	Mode of reproduction	sexual	asexual	sexual	asexual
Genome size	**Flow cytometry [Mb]**	132	213	215	232
	SCROOGE [Mb]	164	228	241	220
Sequencing data	**Sequencing system**	HiSeq2000	HiSeq2000	GAIIx	GAIIx
	Insert size [bp]	300	300	300	300
	Read-length [bp]	100	100	75	75
	Number filtered reads	290119558	274538142	58096450	57360134
	Coverage	~176x	~120x	~16x	~19x
Assemblies	**Assembler**	Platanus	Platanus	Abyss	Abyss
	Number contigs	56361	140559	101559	105693
	N80 [bp]	1440	905	609	561
	N50 [bp]	7410	4184	2446	1557
	Max [bp]	158988	132029	53110	34640
	Sum [bp]	87.47e6	171.8e6	112.6e6	99.84e6

Illumina sequencing and assembly of oribatid mite genomes resulted in fragmented draft genomes with N50 metrics ranging from 1.6 kb to 7.4 kb for scaffolds bigger than 200 bp (Table 1; Supplementary File Ch4SuppAssem). The fragmented state was probably a consequence of using pooled heterozygous individuals from wild populations for sequencing. These assemblies comprise 42% - 82% of the actual genome size.

Table 2: Transposable element library construction and comparison of TE entries > 500bp. Ac: *Achipteria coleoptrata*, Hr: *Hypochthonius rufulus*, Sm: *Steganacarus magnus*, Pp: *Platynothrus peltifer*, Lc: *Leptopilina clavipes*, Dp: *Daphnia pulex*

Species		**Ac**	**Hr**	**Sm**	**Pp**	**Lc**	**Dp**
Total repeats	RepeatModeler	289	600	235	110	-	-
	Tedna	266	218	207	95	-	-
	Combined after UCLUST	450	807	435	205	-	-
Classified TEs	Number of TE sequences	74	117	153	16	162	229
	Number of super-families	10	13	11	7	25	22
	Mean length [bp]	1016	848	999	1176	1886	3108
	Combined length [bp]	75200	99260	152965	18828	305641	711853
	Maximum size [bp]	4838	2505	4665	3899	11311	18820
TEs in assemblies	combined masked [Mb]	0.51	4.47	1.45	0.16	15.01	12.37
	percentage of assembly [%]	0.58	2.59	1.27	0.16	5.86	6.34

Genome-wide repeat comparisons

De novo TE detection methods might fail to identify unknown and old repeats. Therefore, as a general quantification of genome-wide repetitive content between sexual and asexual species and lineages, we calculated the abundance of different 15mers (Fig. 1; Supplementary File Ch4SuppFreq). For *Daphnia*, all four lineages displayed similar 15mer profiles (Fig. 1a). The increase of 150-250 copy 15mers most likely resulted from overrepresented mitochondrial sequences, as the majority of mitochondrial 15mers are found in this range (30% of 15mers mapped to the mitochondrion). In *Leptopilina*, the sexual lineage had slightly more low-to-moderate copy number 15mers (i.e., 8-30; Fig. 1b), whereas the asexual lineage had slightly more moderate-to-high copy 15mers (i.e., 50-150; Fig. 1b). The different oribatid mite species had similar abundances of low-to moderate copy 15mers, except for the sexual *S. magnus* (i.e., 2-25; Fig. 1c). Moderate-to-high copy 15mers were more abundant in sexual *S. magnus* (i.e., 60-200 copies) and A. *coleoptrata* (i.e., 100-200 copies) compared to asexual mites. High-copy 15mers (i.e., 250-350 copies) were less abundant in *P. peltifer* compared to the other three species. Mitochondrial 15mer frequencies were between 100 and 300 copies.

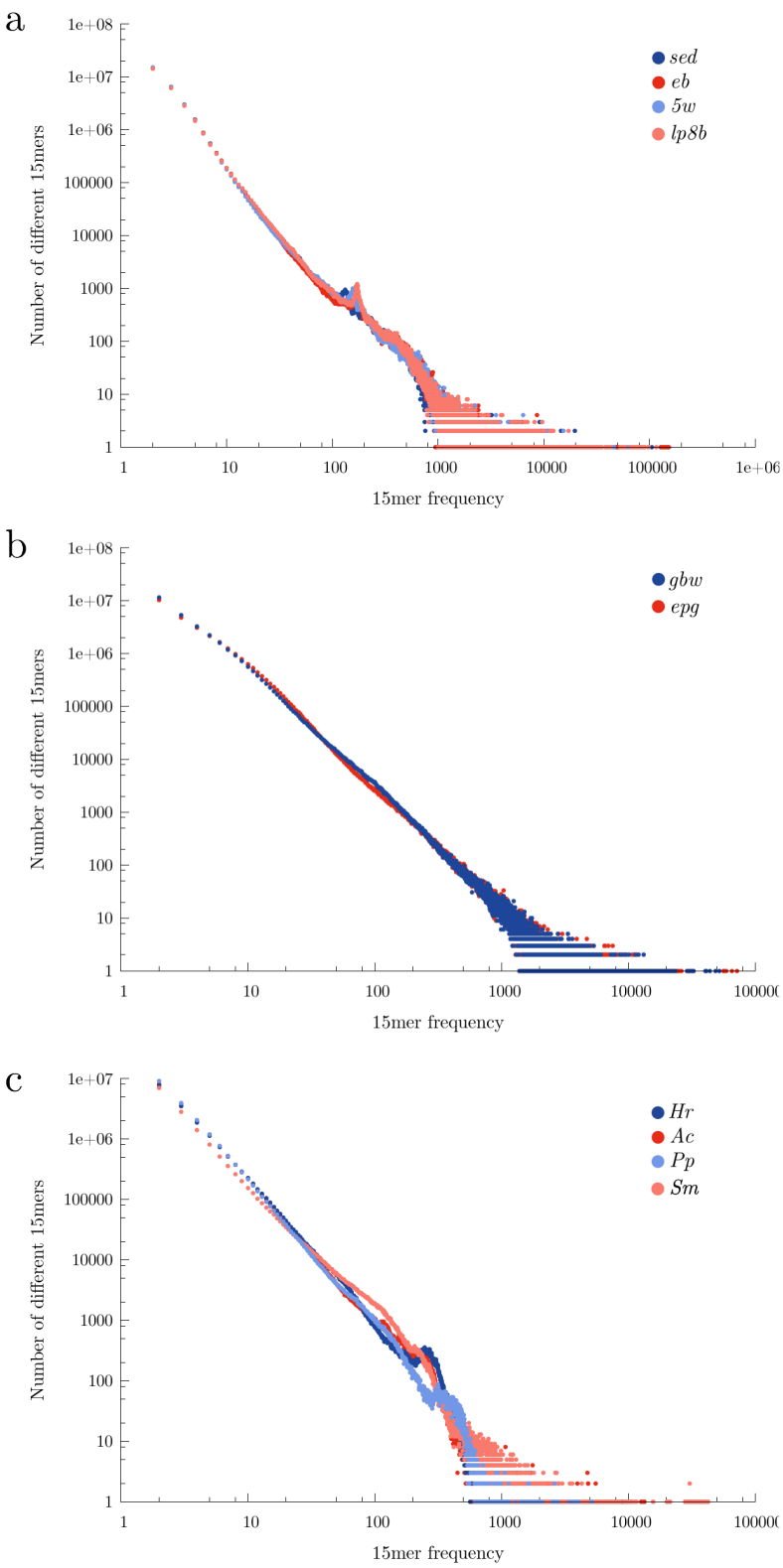

Figure 1: Comparison of overall genomic repetitive content. Frequencies of different 15mers for (a) *Daphnia*, (b) *Leptopilina* and (c) oribatid mite whole genome read data. Asexual species are depicted in blue and sexuals in red. Profiles depict similar repeat content and history for *Daphnia* lineages, whereas in wasps, the asexual contains slightly more recent repeats. All four mite species have different 15mer profiles, with *Steganacarus magnus* (sexual) harboring more and older repeats, *Achipteria coleoptrata* (sexual) and *Hypochthonius rufulus* (asexual) more recent expansions of repeats and fewer and older repeats in *Platynothrus peltifer* (asexual).

Comparison of species-specific TE load

To counter biases in TE *de novo* identification resulting from differences in assemblies, we applied a combined TE detection approach using both assembled and raw read data. Thus, characterized TE metrics were not affected by assembly bias, yielding comparable mean and maximum TE lengths (Table 2). Overall, TE content of oribatid mites inferred in this study was low ($< 2.6\%$). Analysis of the repeat content of genome assemblies might be biased due to the fact that the assembly software potentially pools multiple copies of the same TE into one contig. Furthermore, the quality of different assemblies might vary strongly. To address this bias, we estimated copy numbers of TEs in sexuals and asexuals by calculating read coverage (RPKM values are corrected TE abundances; Supplementary Table S-Ch4.2). RPKM values correlate to genome size ($F_{1,1198} = 111.96$, $P < 0.0001$). We removed this effect by using the residuals from the regression of RPKM on genome size in further analyses.

Overall, RPKM values did not vary significantly with reproductive mode when taxonomic group and TE class were included in the model ($F_{1,1126} = 0.39$, $P = 0.54$). By contrast, the interaction between taxonomic group and TE class was highly significant ($F_{18,1127} = 11.09$, $P < 0.0001$), indicating that taxonomic groups harbor different abundances of the various TE types. For *Daphnia* and *Leptopilina*, we could take advantage of the availability of sister lineages with different reproductive modes, making it possible to directly compare pairs. Again, however, we found no effect of reproductive mode on RPKM values when taking the paired data structure into account (likelihood ratio = 1.16, $P = 0.28$). The four mite species were not organized in pairs. Here, the effect of reproductive mode on RPKM was not significant when controlling for lineage-specific effects ($F_{1,356} = 0.06$, $P = 0.83$).

Although we found no overall difference in TE load between sexuals and asexuals, a small number of specific TEs differed significantly in abundance between closely related sexual and asexual lineages (outliers in Fig. 2a-c). In *Daphnia* and *Leptopilina*, *Gypsy*-like and *Copia*-like LTR elements were more abundant in the asexual lineages compared to sexual sister lineages (Fig. 2a-c). Further, the increase in *Gypsy* in the two *Daphnia* sister-lineages

involved different *Gypsy* elements. In oribatid mites, we found no significant differences among specific elements between sexual and asexual species (Fig. 2d).

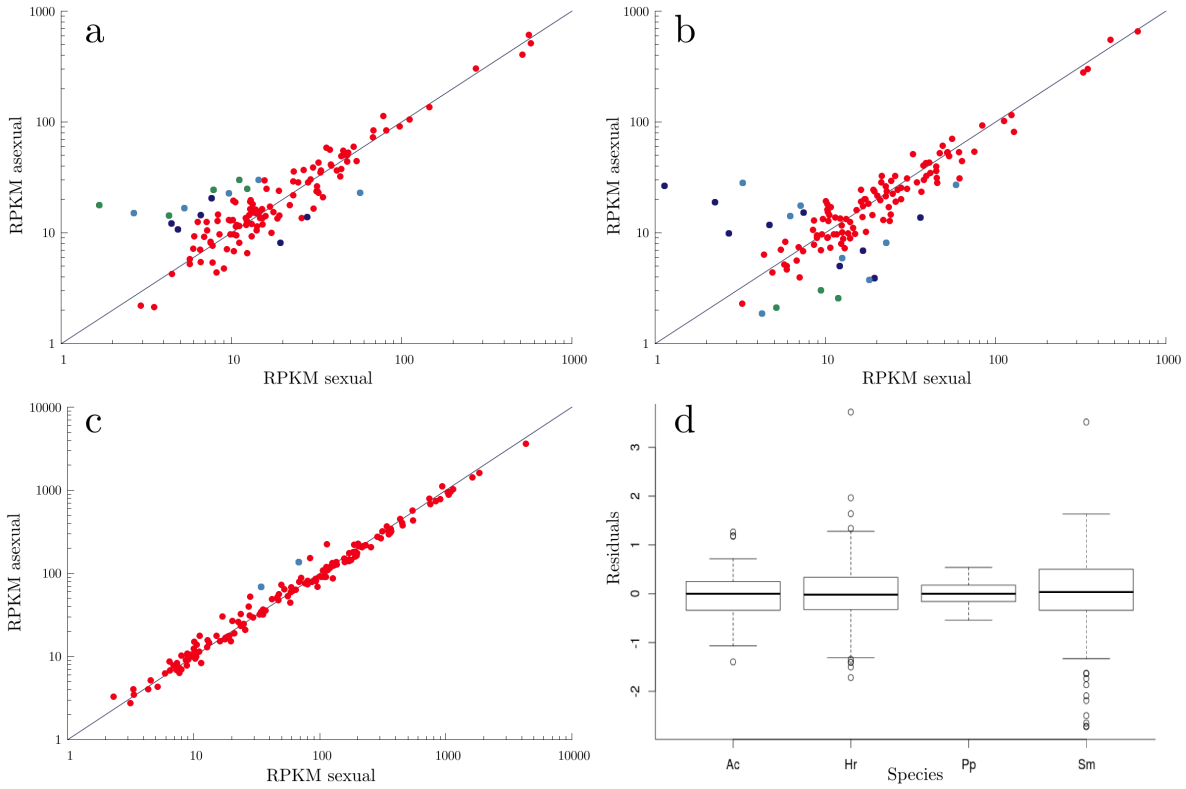

Figure 2: Comparison of TE load between lineages. a,b,c: RPKM values of elements for sexual and asexual (sister) lineages. Each point represents a specific TE library entry. Points above the diagonal line indicates higher load in the asexual lineage and below the line higher TE abundance in the sexual lineage. Blue and green dots indicate at least 2-folder higher RPKM value. Light blue dots are *Gypsy*, dark blue dots are *Copia* and green dots are other elements. (a) *D. pulex eb* and *sed* and (b) *lp8b* and *5w* strains; (c) *Leptopilina clavipes epg* and *gbw* strains. (d) Plot of TE residuals for oribatid mites.

Repeat landscapes

Repeat landscapes (Fig. 3) provided further insights into TE load and activity through time. In the asexual *D. pulex* genome, the most abundant cohorts of TEs were found within 0-6% sequence divergence (Fig. 3a). These were of several major TE classes, with mainly *Gypsy*, *Copia* and *Pao* LTR elements. Other than this, there was no apparent sign of overly increased TE abundance at other sequence divergences. The asexual *L. clavipes* lineage contained most abundant TEs at 2-7% divergence (Fig. 3b). In contrast to TEs in *D. pulex*, TE abundance in *L. clavipes* declined at 1% divergence. The main peak at 0-7% divergence was due to *Gypsy*, *R1*, *Helitron* and *Transib* elements, representing several TE classes. A

second peak found around 17% divergence was due to *PiggyBac* and *TcMar*. Generally, TEs in mites were much less abundant than in *Daphnia* and *Leptopilina*, especially at low divergence (Fig. 3c-f). Some low-to-medium diverged TEs (0-10%) were common in *A. coleoptrata* and *H. rufulus*, but almost no TEs were found within this range in *S. magnus* and *P. peltifer* assemblies. All oribatid mite species showed TE abundance peaks at varying divergence levels. *A. coleoptrata* harbored more continuously diverged elements, while most TEs in *S. magnus* were found at 20-32% divergence. Asexual *H. rufulus* harbored highest TE abundances at around 3% and 16% divergence, mostly due to *Helitron* and *TcMar* elements. The few TEs found in the asexual *P. peltifer* were more divergent than in any other mite. Notably, asexual *H. rufulus* and *P. peltifer* harbor almost no LTR elements (*Gypsy*) compared to sexuals (combined RPKM *Gypsy* values: Sm: 2281, Ac: 1903, Hr: 296, Pp: 67).

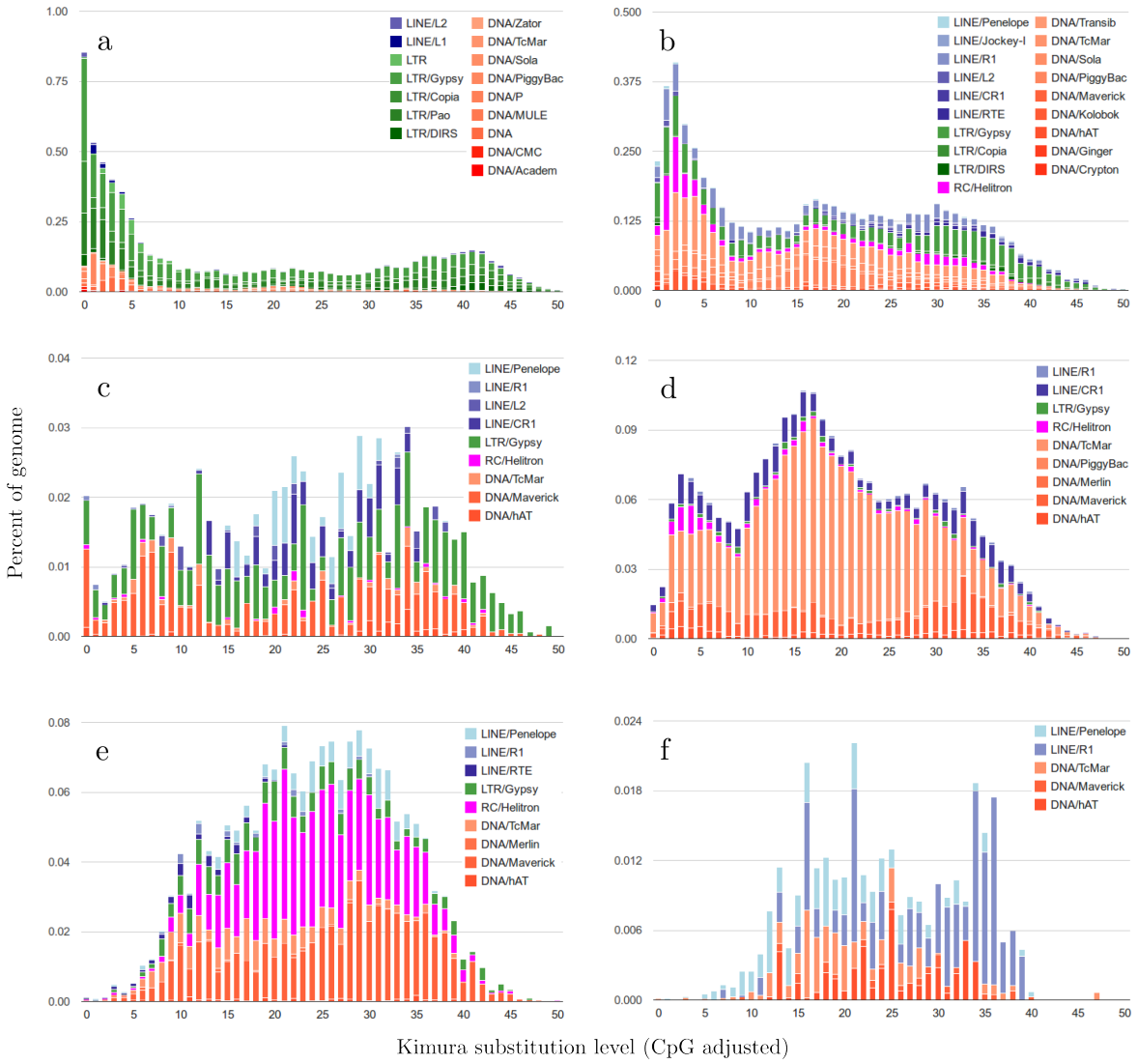

Figure 1: Repeat landscapes depicting the evolutionary history of TE activity for most abundant TE classes in (a) *Drosophila pulex* (asexual genome), (b) *Leptopilina clavipes* (asexual genome), (c) *Achipteria coleoptrata*, (d) *Hypochthonius rufulus*, (e) *Steganacarus magnus* and (f) *Platynothrus peltifer*. Element copies with low divergence from the consensus were recently active, whereas TE copies with older activities are more diverged. Note the different y-axis scales.

Discussion

Overall, repetitive content and lineage-specific TE abundance of recently evolved sister-lineages did not differ with respect to reproductive mode. However, detailed analyses revealed increases in copy numbers for certain TEs within asexual genomes, most pronounced for *Gypsy*-like elements. Generally, TEs were more abundant in *Daphnia* and *Leptopilina* compared to oribatid mites. *Gypsy*-like elements were particularly uncommon in oribatid species under prolonged asexuality. Moreover, in asexual *Daphnia* and *Leptopilina*,

TEs were mainly recently active contrary to generally old TEs in sexual and asexual oribatid mites as indicated by sequence divergence.

Complete repetitive (15mer) content was similar for all *Daphnia* lineages, which suggests similar dynamics and abundance of repeats between sexual and asexual lineages, reflecting their recent separation. For *Leptopilina*, slightly more moderate-to-high copy 15mers in the asexual hint to more recently expanded repeats in the asexual and fewer repeats in the sexual lineage. Oribatid mite kmer profiles were rather lineage-specific. *S. magnus* had more repeats with an older expansion compared to more recent activities in *A. coleoptrata* and *H. rufulus.* The *P. peltifer* profile shows fewer and older repetitive content compared to the other mite species.

In concordance with 15mer profiles, RPKM values, i.e. TE abundances were species-specific. Contrary to our hypotheses, the amount of TEs did not differ between sister-lineages of *Daphnia* and *Leptopilina*, or between oribatid mite species of different reproductive modes. However, some specific *Gypsy* and *Copia* elements had markedly higher copy numbers in asexual *Daphnia* and *Leptopilina* lineages compared to their sexual sister lineages. Further, *Gypsy* expansions involved non-parallel elements in asexual *Daphnia* lineages. For *Leptopilina*, most pronounced changes of outlier TE copy number were found in the asexual lineage. Oribatid mite TE outliers had no pattern, because TE content was too different between species.

Additionally, sequence divergence indicates that TE activity recently increased in the asexual *D. pulex* genome. This burst of activity was mainly the effect of *Gypsy* and *Copia* expansions. There was no sign of other pronounced bursts in the past. The asexual *L. clavipes* lineage also experienced recent TE activity, but contrary to *D. pulex*, this activity declined very recently. Also, several expansions of different TE families occurred in the past, which might reflect some of the repeat expansions in the 15mer profile. For oribatid mites, interpretation of repeat landscapes was more challenging because of the fragmented state of the assemblies and the generally very low TE content. The few elements found in sexual and asexual mites were generally less active recently compared to *Daphnia* and *Leptopilina*. All mite species showed lineage-specific patterns of TE activity. Most pronounced, the asexual *P. peltifer* harbors no apparent recent TE expansions. These

patterns suggest that TEs in in oribatid mites are mostly remnants of past activity and are generally purged from populations no matter if populations reproduce sexually or asexually. Interestingly, *Gypsy* elements almost absent in the repeat landscapes of asexual mites, but were somewhat more abundant in the two sexual species.

Analyses of TE content in other studies are in concordance to the results obtained here. Contrary to the accumulation prediction, and similar to *Capsella* plants that recently became self-compatible (0.1 mya; (Slotte *et al.* 2013), we found no evidence for overall increase of TEs in newly emerged asexual *Daphnia* and *Leptopilina* lineages compared to sexuals. One explanation is that a build-up of TEs might take longer periods of time and accordingly, these lineages might be too recent to experience pronounced TE abundance changes (Dolgin & Charlesworth 2006). However, some LTR elements, especially *Gypsy*, do not follow the overall pattern. One explanation of elevated *Gypsy* elements in newly arisen asexual animals might be that *Gypsy*-like elements are particularly harmful to populations. *Gypsy* elements are closely related to endogenous retroviruses and the only known genetic elements that specifically transpose from the soma to the germline (Burt & Trivers 2006; Lynch 2007). In that way, *Gypsy* elements may potentially induce virus-like dynamics with fast accumulation in asexual populations by spreading and providing resistance at the same time, thereby selecting for maintenance despite deleterious effects (Jalasvuori & Lehtonen 2014). Accordingly, *Gypsy* elements are the first TEs to be active in lineages that recently switched to asexuality.

In concordance with theory, the findings for *Arabidopsis* and *A. vaga*, together with our results from oribatid mite TE analyses suggest that TEs can be lost from asexual lineages over time. In plants, 0.5 myo selfing A. *thaliana* harbored less abundant, less diverse and less active TEs than outcrossing *A. lyrata* (de la Chaux *et al.* 2012; Slotte *et al.* 2013). The reduction in TEs in selfing *A. thaliana* was mostly due to *Gypsy* and *Copia* elements. In animals, the 'asexual' bdelloid rotifer *A. vaga*, being ameiotic for millions of years, contains only few, diverse TEs ($< 3\%$) with only rare full-length copies of recent arrival through horizontal transfer and mostly inactive, old remnants of elements (Flot *et al.* 2013). Very efficient control mechanisms, probably through expansion and diversification of the Dicer and Argonaut/Piwi silencing machinery, are likely efficiently suppressing TEs in these

bdelloid rotifers (Flot *et al.* 2013). Moreover, fitting above predictions for lineages under prolonged asexuality, large population sizes (up to 400,000 ind./m^2; Maraun and Scheu 2000) might explain why TEs in oribatid mites are generally scarce and rather inactive, which was most pronounced for the asexual *P. peltifer*. Interestingly, whole genomes of the bdelloid rotifer and asexual oribatid mites contain none or only very few *Gypsy* elements. This strong selection against these TEs additionally suggests a particularly harmful role of *Gypsy* elements.

Our study suggests that young asexual lineages are do not experience an overall accumulation of transposable elements. However, some specific LTR elements, especially *Gypsy*, increases in copy number in these lineages. Even so *Gypsy* elements and overall TE load can be reduced in asexual populations with large population size and effective control, given enough time.

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II | General Discussion

This thesis investigates the impact of transposable elements as factors contributing to the potential mutational demise of asexual populations. Overall, there is no evidence for TE accumulation in lineages that recently switched to asexuality (**Chapter 4**). However, some idiosyncratic LTR elements (*Gypsy*) show signs of increased load in these lineages, which might be the onset of TE accumulation. On the contrary, taxa under prolonged asexuality harbor only few and inactive TEs (**Chapter 2, 4**). Further, transposable element dynamics are influenced by manifold factors and lineage-specific effects related to each of the animals specific traits and life-styles (Introduction and **Chapter 2, 3, 4**). These results suggest, although likely of deleterious nature, most TEs do not impose an immediate burden on recently arisen asexual lineages and might even be purged under prolonged asexuality.

5.1 TE dynamics

Transposable elements are thought to contribute to the mutational meltdown of asexual lineages via independent replication and predominantly deleterious effects imposed on the host. Here, I found no evidence for TE accumulation in lineages that recently switched to asexuality. Asexual *Daphnia* and *Leptopilina* animals investigated, as well as selfing *Capsella* plants do not harbor an increased load of TEs compared to sexual sister-lineages (**Chapter 4**, Slotte *et al.* 2013). Albeit no overall difference in TE abundance, some idiosyncratic LTR elements, mostly *Gypsy*, have significantly increased copy numbers in these asexual animals. This increase might be due to particularly harmful properties of *Gypsy* elements. Their transposition mechanism involves retrovirus particle formation enabling them to be horizontally transmitted and further, *Gypsy* elements have an increased chance of inheritance by targeting specifically the germ-line. This is the only known genetic element with such a property. Given these characteristics, simulations suggest that *Gypsy* might spread throughout populations and accumulate despite inducing deleterious effects (Jalasvuori & Lehtonen 2014). The germ-line targeted transposition might be also the reason why first changes in TE abundance in newly arisen asexual lineages relate to these elements. Consequently, these asexual lineages might yet be too recent to harbor increased TE loads and might still accumulate TEs over time.

Despite the possibility of TE accumulation, some species that are asexual for extended periods of time show greatly reduced TE abundance and activity compared to overall TE content of most plants and animals (Arkhipova & Rodriguez 2013). *Arabidopsis* plants diminished their TE content since the transition to selfing 0.5 my ago (Slotte *et al.* 2013). More drastically, sexual as well as asexual oribatid mite species and the ameiotic rotifer *A. vaga* contain only very few, mainly inactive TEs (**Chapter 2, 4**). This suggests that these asexuals have effective mechanisms or properties that allow for the containment of TE activity.

5.2 Highly effective TE defence in bdelloid rotifers

The most extensively studied 'asexual' animals are bdelloid rotifers, especially *A. vaga* (**Chapter 2,** Flot *et al.* 2013). Although these rotifers cannot engage in conventional meiosis, they are able to incorporate foreign DNA via horizontal gene transfer (HGT) to a high degree (8% of the genome is of foreign origin). This potentially allows for intra-specific exchange of genetic material. With foreign TEs entering the bdelloid's genome with foreign DNA, rotifers must constantly defend themselves against 'invaders' and *A. vaga* does so very efficiently. As shown in **Chapter 2**, only 3% of its genome consists of highly diverse TEs. These are mostly degraded remnants and the few full-length copies found are most likely of recent arrival. This suggests that TEs are immediately suppressed very efficiently. Responsible might be the greatly expanded and diversified machinery engaging in epigenetic regulation of TEs (**Chapter 2**). Further, extensive gene conversion potentially eliminates TEs from the genome, similar to the purging of deleterious mutations.

5.3 Bdelloid rotifers – eukaryotic bacteria

Despite an ameiotic life-style, *A. vaga* and bdelloid rotifers cannot serve as model-organisms for the evolution of sex anymore, because the findings of **Chapter 2** suggest a bacterial-like, 'open genome' of these eukaryotes, with HGT resembling mixis. After anhydrobiosis bdelloids reshuffle their genomes and integrate environmental DNA (Hespeels *et al.* 2014).

Desiccation degrades the organism's DNA by inducing double-strand breaks (DSB) but *A. vaga* is able to restore a functional genome in short time. Additionally, some genes in bdelloids (e.g., *Spo11*) actively induce DSB and thereby rearrangements of their genomes (Van Doninck & Mark Welch, *personal communicatio*n). Even if not regarded as 'asexual' model-organism anymore, their genome reveals strong selection against TEs, suggesting a deleterious nature of newly arrived elements in these animals.

5.4 Oribatid mites and possible prerequisites for purging TEs

Theories state that harmful TEs potentially are lost from asexual populations given large population sizes and a constant environment (Dolgin & Charlesworth 2006; Startek *et al.* 2013). Oribatid mite population sizes can reach abundances up to 400,000 ind/m^2, which makes them one of the most abundant animal taxon in soil (Maraun & Scheu 2000). Moreover, soil is known to buffer abiotic fluctuations. Accordingly, TEs might be purged, as the least loaded genotypes are not lost and epigenetic TE silencing is not disrupted by stress. Further, oribatid mites differ cytologically from many animals by being automictic and undergoing inverted meiosis with holokinetic chromosomes. This intrinsic property probably maintains heterozygosity and facilitates elimination of TE from genomes (Heethoff *et al.* 2009). Maintained heterozygosity and gene conversion are mechanisms that efficiently purge deleterious elements and mutations from genomes (**Chapter 2**, Flot *et al.* 2013). Thus, low TE content among sexual and asexual oribatid mites probably are a consequence of cytology, populations size and ecology. Strikingly, the animal with the least number of and most inactive TEs was *P. peltifer,* the best studied asexual oribatid mite, which has been named 'ancient asexual scandal' (Heethoff *et al.* 2007).

Oribatid mites comprise several groups with prevalent sexual or asexual reproduction also including congeneric sister pairs that are ecologically similar or different. These species are of varying phylogenetic age including recent asexuals and some under prolonged asexuality (Schaefer *et al.* 2010). Oribatid mites also include species that likely re-evolved sexual reproduction (Domes *et al.* 2007). These manifold characteristics render oribatid mites a unique model system to analyze the consequences of asexual reproduction.

5.5 Species-specific effects on TE dynamics

Transposable element dynamics are influenced by several factors and their dynamics might also be a result of how the transition to asexuality is achieved. Asexuals may not immediately experience unchecked TE proliferation upon the switch to asexuality as epigenetic control mechanisms still suppress preexisting elements (Malone & Hannon 2009; Siomi *et al.* 2011). However, *Wolbachia* in *L. clavipes* potentially hampered epigenetic TE silencing as a side-effect of manipulating cell division, thus facilitating TE activities **Chapter 3**, (Kraaijeveld & Bast 2012b). In order to ensure diploidization and therefore feminization of male wasps, *Wolbachia* likely interferes with the host's meiosis through epigenetic control. Accordingly, previously suppressed and still functional TEs can be reactivated. Evidence for *Wolbachia* interfering with the epigenetic regulation machinery comes from *Aedes aegypti* (Zhang *et al.* 2013). In *Daphnia*, introgression of meiosis-suppressing genetic elements via males might affect TE silencing, as hybridization events can lead to uncontrolled TE proliferation (Ågren 2012; Arkhipova & Rodriguez 2013). Further, gene conversion in asexual *Daphnia* can either lead to the purge or the fixation of TEs at specific genomic loci. Thus, every asexual species has different mechanisms influencing TE dynamics. Genomic investigations of TE content over a range of different sexual and asexual animals facilitate the finding of general patterns, such as the role of *Gypsy* elements in sexual and asexual populations.

5.6 Conclusion

Genetic models predict the demise of asexual lineages through the accumulation of deleterious mutations (mutational meltdown, Muller's ratchet, Kondrashov's hatchet). However, to explain the predominance of sexual reproduction these models are insufficient. The time it takes for asexual organisms to build-up a deleterious mutational load is likely too slow to provide a short-term advantage for sex explaining its predominance (Williams 1975; Maynard Smith 1978; Bell 1982). Potentially imposing a mutational burden acting in recently emerged asexuals, by replicating independently from the cell-cycle, are transposable elements. However, the results of this thesis suggest that TE accumulation, analogous to mutation accumulation, is likely acting too slow to provide this short-term advantage for sex if *Gypsy* element expansion can be contained. Given that asexual species greatly reduce their overall TE content, as well as most harmful TEs over time, threat of extinction resulting from negative fitness effects through TEs might be overcome in some animals given certain prerequisites.

Consequently, acting on short-time scales, this potentially leaves the mixis of genotypes (Weismann 1889) together with ecological models as explanations for the maintenance of sex.

5.7 Perspectives

With the advent of whole genome sequencing, advances in sequencing protocols and computational pipelines for non-model organisms without lab rearings and ever more data made available, the role of TEs in the potential deleterious meltdown of asexual lineages might soon be answered in detail. Moreover, European research networks have formed to integrate different organisms with different levels of relatedness and manifold traits, such as phylogenetic age, cytology and ecology into one holistic hypothetical and methodological framework to seek answers for the evolution of sex in the organisms genomes. Advancing genomics research will allow designing experiments that integrate genetics and ecology of non-model organisms, such as oribatid mites, to elucidate the role of ecology for sexual and asexual reproduction.

IV | Appendix

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig angefertigt, keine unerlaubten Hilfsmittel verwendet und bisher noch keinen Promotionsversuch unternommen habe.

Jens Bast

Göttingen, 17.12.2014

SUPPLEMENTARIES

The complete thesis, original papers and supplementaries for all chapters can be found as digital copy on CD and at:

http://www.jensbast.com/Bast_thesis.zip

Password: Two-Face

Supplementaries Chapter 4

Supplementary scripts

Supplementary script for PClouds frequency calculation.

```
#histogram:
cat out_lumped.txt | cut -d ' ' -f 2 | sort -n | uniq -c > out_lumped.hist
```

Supplementary script for RPKM calculation.

```
#mapping:
ssaha2 -identity 80 -best 1 -kmer 13 -skip 1 -score 12 -cmatch 9 -ckmer 6 -output sam
-outfile OUT.mapped -save UTE reads.fq


#filter reads aligned > 30
cat OUT.mapped.head.sam | awk '{if(substr($1,1,1)!="@"){if
(length($10)>=30)print$0}else{print($0);}}' > UTE.30.sam


#count reads
cat UTE.30.sam | awk ' NF > 0{ counts[$3] = counts[$3] + 1; } END { for (word in counts)
print word, counts[word]; }' | sort > UTE.30.counted


#add TE length
join <(sort UTE.counted) <(sort ../RPKM_analyses/counts/UTE.length.fa) > UTE.30.counted2


#add total reads (collapsed) mapped
cat UTE.counted2 | awk '{print $1,"45085169",$2,$3}' > UTE.counted.table


#calculate RPKM
cat UTE.counted.table | awk '{print $0, (($3)/(($4/1000)*($2/1000000)))}' > UTE.RPKM
```

Supplementary script Ch4SuppR for statistics.

```
rpkm_GS <- read.table("/home/jensbast/Dropbox/cooperation_asexuals/RPKM_new/ALL.R.stats.GS",
header=T)
View(rpkm_GS)

# check correlation between rpkm and genome size
m0 <-lm(log(rpkm)~genome_size, data=rpkm_GS)
summary(m0)
aov(m0)
anova(m0, test="F")
plot(m0)
plot(log(rpkm)~genome_size, data=rpkm_GS)
with(rpkm_GS, cor.test(log(rpkm),genome_size))
# turns out to be highly correlated

m01 <-lm(log(rpkm)~sex_asex*genome_size, data=rpkm_GS)
m02 <-lm(log(rpkm)~sex_asex+genome_size, data=rpkm_GS)
m03 <-lm(log(rpkm)~sex_asex, data=rpkm_GS)
m04 <-lm(log(rpkm)~genome_size, data=rpkm_GS)
anova(m01,m02,test="F")
anova(m02,m03,test="F")
anova(m02,m04,test="F")
# sex/asex explains some variation when you control for genome size

m010 <-lm(log(rpkm)~te_class*genome_size, data=rpkm_GS)
m011 <-lm(log(rpkm)~te_class+genome_size, data=rpkm_GS)
anova(m010,m011,test="F")
# significant interaction between genome size and te_class
# some TEs contribute more to genome size than others?

m020 <-lm(log(rpkm)~tax_group*genome_size, data=rpkm_GS)
m021 <-lm(log(rpkm)~tax_group+genome_size, data=rpkm_GS)
anova(m020,m021,test="F")
# this doesn't seem to work
# interaction seems to explain everything?

m030 <-lm(log(rpkm)~sex_asex*te_class*genome_size, data=rpkm_GS)
aov(m030)
m031 <-lm(log(rpkm)~sex_asex*te_class*genome_size-sex_asex:te_class:genome_size,
data=rpkm_GS)
anova(m030,m031,test="F")
# three-way interaction significant...

# extract residuals
resid <-residuals(lm(log(rpkm)~genome_size, data=rpkm_GS))
```

```
# Repeat analysis on residuals
m040 <- lm(resid~sex_asex, data=rpkm_GS)
summary(m040)
# effect of sex/asex the same
m041 <-lm(resid~te_class, data=rpkm_GS)
summary(m041)
aov(m041)

m042 <-lm(resid~tax_group, data=rpkm_GS)
summary(m042)
# this now gives a model - all tax_groups significantly different

# explanatory variables combined
# removing factors one by one, starting with the highest-order interaction
m043 <-lm(resid~tax_group*sex_asex*te_class, data=rpkm_GS)
aov(m043)
m044 <-lm(resid~tax_group*sex_asex*te_class-tax_group:sex_asex:te_class, data=rpkm_GS)
anova(m043,m044, test="F")
m045 <-lm(resid~tax_group*sex_asex*te_class-tax_group:sex_asex:te_class-tax_group:sex_asex,
data=rpkm_GS)
anova(m044,m045, test="F")
aov(m045)
m046 <-lm(resid~tax_group*sex_asex*te_class-tax_group:sex_asex:te_class-tax_group:sex_asex-
sex_asex:te_class, data=rpkm_GS)
anova(m045,m046, test="F")
m047 <-lm(resid~tax_group+sex_asex+te_class, data=rpkm_GS)
anova(m046,m047, test="F")

# only the tax_group:te_class interaction is significant
# removing main effect of sex_asex
m048 <-lm(resid~tax_group*te_class, data=rpkm_GS)
anova(m048,m046,test="F")
summary(m046)

# checking what removes the sex_asex effect
m049 <-lm(resid~tax_group+sex_asex, data=rpkm_GS)
m050 <-lm(resid~tax_group, data=rpkm_GS)
anova(m049,m050)
m051 <-lm(resid~te_class+sex_asex, data=rpkm_GS)
m052 <-lm(resid~te_class, data=rpkm_GS)
anova(m051,m052)
# so, the conclusion is that there is a small effect of sex_asex when you control for genome
size
# but this effect disappears when you include tax_group or te_class

# Finding a final model
m053 <-lm(resid~tax_group*te_class, data=rpkm_GS)
m054 <-lm(resid~tax_group+te_class, data=rpkm_GS)
anova(m053,m054)
```

```
#------------------------------------------------------------


# the same analysis, but now taking the paired data structure into account

# can only do this for lclav and daphnia

library(nlme)


# first a model with taxonomic group and sex/asex as explanatory variables

# including TE class doesn't work, because we have only 1 for some TEs

m10 <- lme(log(rpkm)~tax_group*sex_asex, random=~1|te_unique, data=rpkm_GS,
subset=c(tax_group=="Lclav" | tax_group=="Daphnia"))

summary(m10)


# the interaction term is not significant, so we drop it from the model

m11 <- lme(log(rpkm)~tax_group+sex_asex, random=~1|te_unique, data=rpkm_GS,
subset=c(tax_group=="Lclav" | tax_group=="Daphnia"))

summary(m11)


# sex/asex is not significant, so we drop this too

m12 <- lme(log(rpkm)~tax_group, random=~1|te_unique, data=rpkm_GS,
subset=c(tax_group=="Lclav" | tax_group=="Daphnia"))

summary(m12)


# compare models

m11a <- lme(log(rpkm)~tax_group+sex_asex, random=~1|te_unique, data=rpkm_GS,
subset=c(tax_group=="Lclav" | tax_group=="Daphnia"), method="ML")

m12a <- lme(log(rpkm)~tax_group, random=~1|te_unique, data=rpkm_GS,
subset=c(tax_group=="Lclav" | tax_group=="Daphnia"), method="ML")

anova(m11a,m12a)


# Result: Daphnia and clavipes differ in their TE content

# no effect of sex/asex

plot(m12)


# the plot shows some outliers (large residuals). These could be of interest

# model the effect of sex/asex for Daphnia and clavipes independently

m13 <- lme(log(rpkm)~sex_asex, random=~1|te_unique, data=rpkm_GS,
subset=c(tax_group=="Daphnia"))

summary(m13)

plot(m13, id=0.05)

m14 <- lme(log(rpkm)~sex_asex, random=~1|te_unique, data=rpkm_GS,
subset=c(tax_group=="Lclav"))

summary(m14)

plot(m14, id=0.05)


# identify the outliers

which(abs(residuals(m13,type="normalized"))>qnorm(0.975))

which(abs(residuals(m14,type="normalized"))>qnorm(0.975))
```

```
#-------------------------------------------------------------
# We can't construct paired models for the mites, so we switch back to linear models
# sex/asex and and overlap, so we can't combine them in one model
# look at sex/asex first
m20 <- lm(log(rpkm)~sex_asex*te_class+genome_size, data=rpkm_GS, subset=c(tax_group=="Ori"))
summary(m20)
aov(m20)

resid_mites <- residuals(lm(log(rpkm)~genome_size, data=rpkm_GS,
subset=c(tax_group=="Ori")))

# drop the interaction term
m21 <- lm(log(rpkm)~sex_asex+te_class+genome_size, data=rpkm_GS, subset=c(tax_group=="Ori"))
anova(m20,m21, test="F")

# the interaction is significant
# sex and asex mites seem to have different TE abundances
# Replace sex/asex by species
m22 <- lm(log(rpkm)~species*te_class+genome_size, data=rpkm_GS, subset=c(tax_group=="Ori"))
m23 <- lm(log(rpkm)~species+te_class+genome_size, data=rpkm_GS, subset=c(tax_group=="Ori"))
anova(m22,m23, test="F")
plot(m22)

# again, the interaction is significant
# the different mite species have different TE abundances
# look at some of the outliers
rpkm_GS[1107,] # penelope
rpkm_GS[1029,] # TcMar
rpkm_GS[1051,] # gypsy

which(abs(residuals(m20,type="normalized"))>qnorm(0.975))
plot(resid_mites)
plot(log(rpkm_GS$rpkm)~rpkm_GS$species, subset=c(rpkm_GS$tax_group=="Ori"))

# try model with species as random effect
m061 <- lme(log(rpkm)~sex_asex, random=~1|species, data=rpkm_GS, subset=c(tax_group=="Ori"))
summary(m061)
anova(m061)
plot(m061)

# m22 explains most of the variance in the mite data
# create new dataframe for mites
# take the residuals and add to data frame
# reset factor levels for species
rpkm_mites <- subset(rpkm_GS, tax_group=="Ori")
rpkm_mites$resid <- residuals(m22)
rpkm_mites$species <- factor(rpkm_mites$species)
plot(rpkm_mites$species,rpkm_mites$resid)
```

Supplementary Figures

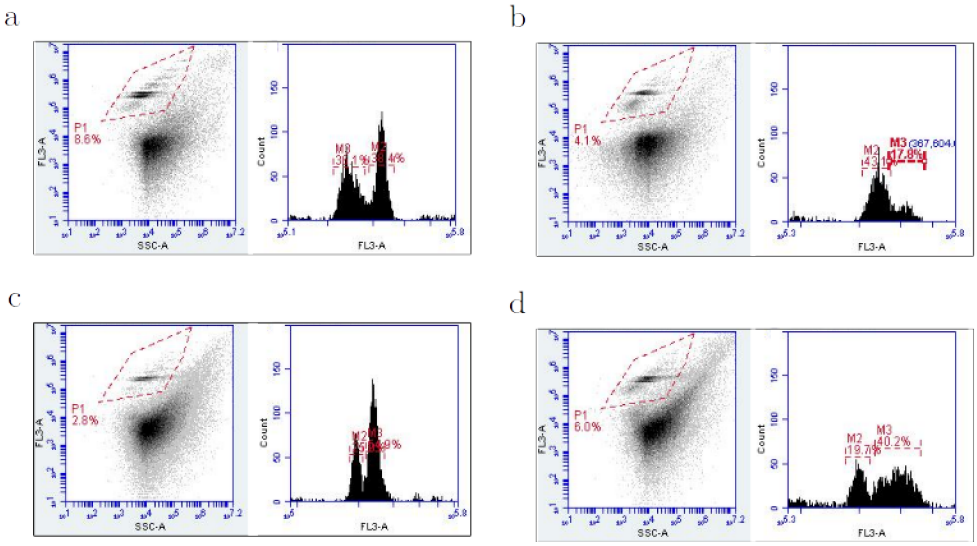

Figure S-Ch4.1: Flow cytometry cell counts and fluorescence for (a) *Achipteria coleoptrata*, (b) *Hypochthonius rufulus*, (c) *Steganacarus magnus* and (d) *Platynothrus peltifer*. The left panel depicts the overall cells counted for co-stained oribatid mites and *Drosophila melanogaster*. Cells in the range of mite and fly nuclei are selected on the right panel for fluorescence comparisons.

Supplementary Tables

Table S-Ch4.1: Genome size estimates for all four oribatid mite species using flow cytometry data and the formular $GS_{mite} = GS_{fly}$ x PI-fluor$_{mite}$ / PI-fluor$_{fly}$.

Species		**Sm**	Dm	**Ac**	Dm	**Hr**	Dm	**Pp**	Dm
Fluorescence peaks	2C	408	332	244	323	418	343	395	298
	4C	848	662	508	663	841	685	789	596
Haploid genome size [Mb]		**215**		**132**		**213**		**232**	

Table S-Ch4.2: RPKM values for each TE library entry together with TE class, taxonomic group, species or lineage and genome size used for statistical TE comparisons.

rpkm	sex_asex	te_class	tax_group	species	te_unique	genome_size
24.4505	asex	Academ	Daphnia	Dpu_5w2	Academ-1_DPu_lpb_5w	200
14.4796	asex	BEL	Daphnia	Dpu_5w2	BEL-10_DPu-I_lpb_5w	200
30.8588	asex	BEL	Daphnia	Dpu_5w2	BEL-11_DPu-I_lpb_5w	200
52.4524	asex	BEL	Daphnia	Dpu_5w2	BEL-12_DPu-I_lpb_5w	200
6.32164	asex	BEL	Daphnia	Dpu_5w2	BEL-13_DPu-I_lpb_5w	200
28.2092	asex	BEL	Daphnia	Dpu_5w2	BEL-14_DPu-I_lpb_5w	200
15.9891	asex	BEL	Daphnia	Dpu_5w2	BEL-15_DPu-I_lpb_5w	200
19.0785	asex	BEL	Daphnia	Dpu_5w2	BEL-16_DPu-I_lpb_5w	200
28487	asex	BEL	Daphnia	Dpu_5w2	BEL-17_DPu-I_lpb_5w	200
14.6177	asex	BEL	Daphnia	Dpu_5w2	BEL-18_DPu-I_lpb_5w	200
12.8941	asex	BEL	Daphnia	Dpu_5w2	BEL-19_DPu-I_lpb_5w	200
3.94424	asex	BEL	Daphnia	Dpu_5w2	BEL-1_DPu-I_lpb_5w	200
3.04391	asex	BEL	Daphnia	Dpu_5w2	BEL-2_DPu-I_lpb_5w	200
32.4802	asex	BEL	Daphnia	Dpu_5w2	BEL-3_DPu-I_lpb_5w	200
53.2232	asex	BEL	Daphnia	Dpu_5w2	BEL-4_DPu-I_lpb_5w	200
2.56336	asex	BEL	Daphnia	Dpu_5w2	BEL-5_DPu-I_lpb_5w	200
7.02544	asex	BEL	Daphnia	Dpu_5w2	BEL-6_DPu-I_lpb_5w	200
13.7382	asex	BEL	Daphnia	Dpu_5w2	BEL-7_DPu-I_lpb_5w	200
20.0984	asex	BEL	Daphnia	Dpu_5w2	BEL-8_DPu-I_lpb_5w	200
28.6597	asex	BEL-9	Daphnia	Dpu_5w2	BEL-9_DPu_lpb_5w	200
7.24384	asex	Copia	Daphnia	Dpu_5w2	Copia-10_DPu-I_lpb_5w	200
9.00482	asex	Copia	Daphnia	Dpu_5w2	Copia-11_DPu-I_lpb_5w	200
11825	asex	Copia	Daphnia	Dpu_5w2	Copia-12_DPu-I_lpb_5w	200
13.0643	asex	Copia	Daphnia	Dpu_5w2	Copia-13_DPu-I_lpb_5w	200
22.6075	asex	Copia	Daphnia	Dpu_5w2	Copia-14_DPu-I_lpb_5w	200
5.03039	asex	Copia	Daphnia	Dpu_5w2	Copia-15_DPu-I_lpb_5w	200
9.75273	asex	Copia	Daphnia	Dpu_5w2	Copia-16_DPu-I_lpb_5w	200
25.0294	asex	Copia	Daphnia	Dpu_5w2	Copia-17_DPu-I_lpb_5w	200
8.91054	asex	Copia	Daphnia	Dpu_5w2	Copia-18_DPu-I_lpb_5w	200
5.00213	asex	Copia	Daphnia	Dpu_5w2	Copia-19_DPu-I_lpb_5w	200
7.43037	asex	Copia	Daphnia	Dpu_5w2	Copia-1_DPu-I_lpb_5w	200
15.3099	asex	Copia	Daphnia	Dpu_5w2	Copia-20_DPu-I_lpb_5w	200
10.1807	asex	Copia	Daphnia	Dpu_5w2	Copia-21_DPu-I_lpb_5w	200
16.1993	asex	Copia	Daphnia	Dpu_5w2	Copia-22_DPu-I_lpb_5w	200
14.4074	asex	Copia	Daphnia	Dpu_5w2	Copia-23_DPu-I_lpb_5w	200
15.2554	asex	Copia	Daphnia	Dpu_5w2	Copia-24_DPu-I_lpb_5w	200
13.6861	asex	Copia	Daphnia	Dpu_5w2	Copia-25_DPu-I_lpb_5w	200
17.0082	asex	Copia	Daphnia	Dpu_5w2	Copia-26_DPu-I_lpb_5w	200
31.0465	asex	Copia	Daphnia	Dpu_5w2	Copia-27_DPu-I_lpb_5w	200
13926	asex	Copia	Daphnia	Dpu_5w2	Copia-28_DPu-I_lpb_5w	200
29.9008	asex	Copia	Daphnia	Dpu_5w2	Copia-29_DPu-I_lpb_5w	200
13.3413	asex	Copia	Daphnia	Dpu_5w2	Copia-2_DPu-I_lpb_5w	200
4.38953	asex	Copia	Daphnia	Dpu_5w2	Copia-30_DPu-I_lpb_5w	200
12.8329	asex	Copia	Daphnia	Dpu_5w2	Copia-31_DPu-I_lpb_5w	200
6.88185	asex	Copia	Daphnia	Dpu_5w2	Copia-32_DPu-I_lpb_5w	200
9.9045	asex	Copia	Daphnia	Dpu_5w2	Copia-33_DPu-I_lpb_5w	200
3.91007	asex	Copia	Daphnia	Dpu_5w2	Copia-34_DPu-I_lpb_5w	200
29.5075	asex	Copia	Daphnia	Dpu_5w2	Copia-35_DPu-I_lpb_5w	200
5.16389	asex	Copia	Daphnia	Dpu_5w2	Copia-36_DPu-I_lpb_5w	200

20.1943 asex	Copia	Daphnia	Dpu_5w2	Copia-37_DPu-I_lpb_5w	200
9.70343 asex	Copia	Daphnia	Dpu_5w2	Copia-38_DPu-I_lpb_5w	200
13.4686 asex	Copia	Daphnia	Dpu_5w2	Copia-39_DPu-I_lpb_5w	200
26.5233 asex	Copia	Daphnia	Dpu_5w2	Copia-3_DPu-I_lpb_5w	200
2.29763 asex	Copia	Daphnia	Dpu_5w2	Copia-4_DPu-I_lpb_5w	200
26.2677 asex	Copia	Daphnia	Dpu_5w2	Copia-5_DPu-I_lpb_5w	200
18.8526 asex	Copia	Daphnia	Dpu_5w2	Copia-6_DPu-I_lpb_5w	200
19.5962 asex	Copia	Daphnia	Dpu_5w2	Copia-7_DPu-I_lpb_5w	200
13.3442 asex	Copia	Daphnia	Dpu_5w2	Copia-8_DPu-I_lpb_5w	200
7.81852 asex	Copia	Daphnia	Dpu_5w2	Copia-9_DPu-I_lpb_5w	200
10045 asex	DIRS	Daphnia	Dpu_5w2	DIRS-1_DPu_lpb_5w	200
21661 asex	DIRS	Daphnia	Dpu_5w2	DIRS-2_DPu_lpb_5w	200
10.6214 asex	DIRS	Daphnia	Dpu_5w2	DIRS-3_DPu_lpb_5w	200
18.3795 asex	DIRS	Daphnia	Dpu_5w2	DIRS-4_DPu_lpb_5w	200
9.44731 asex	DIRS	Daphnia	Dpu_5w2	DIRS-5_DPu_lpb_5w	200
17.0607 asex	DIRS	Daphnia	Dpu_5w2	DIRS-6_DPu_lpb_5w	200
549.12 asex	DNA	Daphnia	Dpu_5w2	DNA-1_DPu_lpb_5w	200
53.1766 asex	DNA2	Daphnia	Dpu_5w2	DNA2-1_DPu_lpb_5w	200
657523 asex	DNA	Daphnia	Dpu_5w2	DNA-2_DPu_lpb_5w	200
52.6426 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-10_DPu-I_lpb_5w	200
31.4043 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-11_DPu-I_lpb_5w	200
5.90048 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-12_DPu-I_lpb_5w	200
12.5014 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-13_DPu-I_lpb_5w	200
25.5269 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-14_DPu-I_lpb_5w	200
17.5247 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-15_DPu-I_lpb_5w	200
5.63064 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-16_DPu-I_lpb_5w	200
0.755259 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-17_DPu-I_lpb_5w	200
1.85963 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-18_DPu-I_lpb_5w	200
18.1995 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-19_DPu-I_lpb_5w	200
3.74501 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-1_DPu-I_lpb_5w	200
21.3114 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-1-I_DP_lpb_5w	200
44.5117 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-1-LTR_DP_lpb_5w	200
49.3717 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-21_DPu-I_lpb_5w	200
39.4424 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-22_DPu-I_lpb_5w	200
24.4278 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-23_DPu-I_lpb_5w	200
17.3937 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-24_DPu-I_lpb_5w	200
28.2724 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-25_DPu-I_lpb_5w	200
51.0395 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-26_DPu-I_lpb_5w	200
42.4954 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-27_DPu-I_lpb_5w	200
23.6184 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-28_DPu-I_lpb_5w	200
8.10004 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-29_DPu-I_lpb_5w	200
8.27653 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-2_DPu-I_lpb_5w	200
9.92118 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-2-I_DP_lpb_5w	200
81.1316 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-2-LTR_DP_lpb_5w	200
14.1007 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-30_DPu-I_lpb_5w	200
23.3952 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-31_DPu-I_lpb_5w	200
40.5686 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-32_DPu-I_lpb_5w	200
12734 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-33_DPu-I_lpb_5w	200
24.3293 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-34_DPu-I_lpb_5w	200
32.4632 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-35_DPu-I_lpb_5w	200
9.64329 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-36_DPu-I_lpb_5w	200
92.8472 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-37_DPu-I_lpb_5w	200
8.83412 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-38_DPu-I_lpb_5w	200
9.08592 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-39_DPu-I_lpb_5w	200
36.0753 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-3_DPu-I_lpb_5w	200
53.9817 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-40_DPu-I_lpb_5w	200
19.3431 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-4_DPu-I_lpb_5w	200
4.67991 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-5_DPu-I_lpb_5w	200
20.0442 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-6_DPu-I_lpb_5w	200
9.67048 asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-7_DPu-I_lpb_5w	200

34.6824	asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-8_DPu-I_lpb_5w	200
19.0357	asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-9_DPu-I_lpb_5w	200
27.1367	asex	Gypsy	Daphnia	Dpu_5w2	Gypsy-N1_DPu-I_lpb_5w	200
70.6745	asex	L2	Daphnia	Dpu_5w2	L2-1_DPu_lpb_5w	200
300576	asex	LT1	Daphnia	Dpu_5w2	LT1_DPu-I_lpb_5w	200
23.6793	asex	LT2	Daphnia	Dpu_5w2	LT2_DPu-I_lpb_5w	200
42.8492	asex	Mariner	Daphnia	Dpu_5w2	Mariner-1_DPu_lpb_5w	200
11.0488	asex	MuDR	Daphnia	Dpu_5w2	MuDR-1_DPu_lpb_5w	200
11.6829	asex	MuDRF	Daphnia	Dpu_5w2	MuDRF-1_DPu_lpb_5w	200
6.98385	asex	Nimb	Daphnia	Dpu_5w2	Nimb-1_DPu_lpb_5w	200
32.5886	asex	P	Daphnia	Dpu_5w2	P-1_DPu_lpb_5w	200
101745	asex	piggyBac	Daphnia	Dpu_5w2	piggyBac-1_DPu_lpb_5w	200
115871	asex	POKEY	Daphnia	Dpu_5w2	POKEY_DP_lpb_5w	200
2.12107	asex	Sola1	Daphnia	Dpu_5w2	Sola1-1_DPu_lpb_5w	200
6.85501	asex	Sola2	Daphnia	Dpu_5w2	Sola2-1_DPu_lpb_5w	200
7.34119	asex	Sola2	Daphnia	Dpu_5w2	Sola2-2_DPu_lpb_5w	200
60.8476	asex	Sola2	Daphnia	Dpu_5w2	Sola2-3_DPu_lpb_5w	200
9.02967	asex	Sola3	Daphnia	Dpu_5w2	Sola3-1_DPu_lpb_5w	200
281035	asex	Tx1	Daphnia	Dpu_5w2	Tx1-1_DPu_lpb_5w	200
8.00847	asex	Zator	Daphnia	Dpu_5w2	Zator-1_DPu_lpb_5w	200
24.6876	sex	Academ	Daphnia	Dpu_eb1	Academ-1_DPu_eb_sed	200
18.5684	sex	BEL	Daphnia	Dpu_eb1	BEL-10_DPu-I_eb_sed	200
45.3103	sex	BEL	Daphnia	Dpu_eb1	BEL-11_DPu-I_eb_sed	200
67548	sex	BEL	Daphnia	Dpu_eb1	BEL-12_DPu-I_eb_sed	200
8.14894	sex	BEL	Daphnia	Dpu_eb1	BEL-13_DPu-I_eb_sed	200
33.5712	sex	BEL	Daphnia	Dpu_eb1	BEL-14_DPu-I_eb_sed	200
7.13666	sex	BEL	Daphnia	Dpu_eb1	BEL-15_DPu-I_eb_sed	200
12.3565	sex	BEL	Daphnia	Dpu_eb1	BEL-16_DPu-I_eb_sed	200
41.6136	sex	BEL	Daphnia	Dpu_eb1	BEL-17_DPu-I_eb_sed	200
43.4689	sex	BEL	Daphnia	Dpu_eb1	BEL-18_DPu-I_eb_sed	200
11.1203	sex	BEL	Daphnia	Dpu_eb1	BEL-19_DPu-I_eb_sed	200
8.99553	sex	BEL	Daphnia	Dpu_eb1	BEL-1_DPu-I_eb_sed	200
6.03542	sex	BEL	Daphnia	Dpu_eb1	BEL-2_DPu-I_eb_sed	200
15.6688	sex	BEL	Daphnia	Dpu_eb1	BEL-3_DPu-I_eb_sed	200
44.2669	sex	BEL	Daphnia	Dpu_eb1	BEL-4_DPu-I_eb_sed	200
7.72992	sex	BEL	Daphnia	Dpu_eb1	BEL-5_DPu-I_eb_sed	200
6.59065	sex	BEL	Daphnia	Dpu_eb1	BEL-6_DPu-I_eb_sed	200
13.2722	sex	BEL	Daphnia	Dpu_eb1	BEL-7_DPu-I_eb_sed	200
23.1574	sex	BEL	Daphnia	Dpu_eb1	BEL-8_DPu-I_eb_sed	200
33.2297	sex	BEL-9	Daphnia	Dpu_eb1	BEL-9_DPu_eb_sed	200
13.1216	sex	Copia	Daphnia	Dpu_eb1	Copia-10_DPu-I_eb_sed	200
10.3028	sex	Copia	Daphnia	Dpu_eb1	Copia-11_DPu-I_eb_sed	200
11.1248	sex	Copia	Daphnia	Dpu_eb1	Copia-12_DPu-I_eb_sed	200
12.8925	sex	Copia	Daphnia	Dpu_eb1	Copia-13_DPu-I_eb_sed	200
26.5259	sex	Copia	Daphnia	Dpu_eb1	Copia-14_DPu-I_eb_sed	200
10.3479	sex	Copia	Daphnia	Dpu_eb1	Copia-15_DPu-I_eb_sed	200
13.2479	sex	Copia	Daphnia	Dpu_eb1	Copia-16_DPu-I_eb_sed	200
19.0042	sex	Copia	Daphnia	Dpu_eb1	Copia-17_DPu-I_eb_sed	200
7.5544	sex	Copia	Daphnia	Dpu_eb1	Copia-18_DPu-I_eb_sed	200
7.71842	sex	Copia	Daphnia	Dpu_eb1	Copia-19_DPu-I_eb_sed	200
7.52992	sex	Copia	Daphnia	Dpu_eb1	Copia-1_DPu-I_eb_sed	200
25.8915	sex	Copia	Daphnia	Dpu_eb1	Copia-20_DPu-I_eb_sed	200
15.1934	sex	Copia	Daphnia	Dpu_eb1	Copia-21_DPu-I_eb_sed	200
4.84503	sex	Copia	Daphnia	Dpu_eb1	Copia-22_DPu-I_eb_sed	200
12.1493	sex	Copia	Daphnia	Dpu_eb1	Copia-23_DPu-I_eb_sed	200
10.2481	sex	Copia	Daphnia	Dpu_eb1	Copia-24_DPu-I_eb_sed	200
23.1315	sex	Copia	Daphnia	Dpu_eb1	Copia-25_DPu-I_eb_sed	200
15.2221	sex	Copia	Daphnia	Dpu_eb1	Copia-26_DPu-I_eb_sed	200
14.0201	sex	Copia	Daphnia	Dpu_eb1	Copia-27_DPu-I_eb_sed	200
6.60132	sex	Copia	Daphnia	Dpu_eb1	Copia-28_DPu-I_eb_sed	200

38.2203 sex	Copia	Daphnia	Dpu_eb1	Copia-29_DPu-I_eb_sed	200
9.61983 sex	Copia	Daphnia	Dpu_eb1	Copia-2_DPu-I_eb_sed	200
4.43501 sex	Copia	Daphnia	Dpu_eb1	Copia-30_DPu-I_eb_sed	200
6.31133 sex	Copia	Daphnia	Dpu_eb1	Copia-31_DPu-I_eb_sed	200
13.1746 sex	Copia	Daphnia	Dpu_eb1	Copia-32_DPu-I_eb_sed	200
6.52546 sex	Copia	Daphnia	Dpu_eb1	Copia-33_DPu-I_eb_sed	200
19.3112 sex	Copia	Daphnia	Dpu_eb1	Copia-34_DPu-I_eb_sed	200
31.9506 sex	Copia	Daphnia	Dpu_eb1	Copia-35_DPu-I_eb_sed	200
5.68868 sex	Copia	Daphnia	Dpu_eb1	Copia-36_DPu-I_eb_sed	200
32.4894 sex	Copia	Daphnia	Dpu_eb1	Copia-37_DPu-I_eb_sed	200
9.38899 sex	Copia	Daphnia	Dpu_eb1	Copia-38_DPu-I_eb_sed	200
14.7464 sex	Copia	Daphnia	Dpu_eb1	Copia-39_DPu-I_eb_sed	200
7.62546 sex	Copia	Daphnia	Dpu_eb1	Copia-3_DPu-I_eb_sed	200
3.51789 sex	Copia	Daphnia	Dpu_eb1	Copia-4_DPu-I_eb_sed	200
27753 sex	Copia	Daphnia	Dpu_eb1	Copia-5_DPu-I_eb_sed	200
11.1406 sex	Copia	Daphnia	Dpu_eb1	Copia-6_DPu-I_eb_sed	200
13.8949 sex	Copia	Daphnia	Dpu_eb1	Copia-7_DPu-I_eb_sed	200
15.1247 sex	Copia	Daphnia	Dpu_eb1	Copia-8_DPu-I_eb_sed	200
10.6617 sex	Copia	Daphnia	Dpu_eb1	Copia-9_DPu-I_eb_sed	200
10.5982 sex	DIRS	Daphnia	Dpu_eb1	DIRS-1_DPu_eb_sed	200
16.8018 sex	DIRS	Daphnia	Dpu_eb1	DIRS-2_DPu_eb_sed	200
8.2796 sex	DIRS	Daphnia	Dpu_eb1	DIRS-3_DPu_eb_sed	200
30.2448 sex	DIRS	Daphnia	Dpu_eb1	DIRS-4_DPu_eb_sed	200
7.16705 sex	DIRS	Daphnia	Dpu_eb1	DIRS-5_DPu_eb_sed	200
17.6805 sex	DIRS	Daphnia	Dpu_eb1	DIRS-6_DPu_eb_sed	200
574576 sex	DNA	Daphnia	Dpu_eb1	DNA-1_DPu_eb_sed	200
52181 sex	DNA2	Daphnia	Dpu_eb1	DNA2-1_DPu_eb_sed	200
557928 sex	DNA	Daphnia	Dpu_eb1	DNA-2_DPu_eb_sed	200
48.3827 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-10_DPu-I_eb_sed	200
9.63724 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-11_DPu-I_eb_sed	200
10.1869 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-12_DPu-I_eb_sed	200
10.7726 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-13_DPu-I_eb_sed	200
19.1425 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-14_DPu-I_eb_sed	200
13.8614 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-15_DPu-I_eb_sed	200
5.66988 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-16_DPu-I_eb_sed	200
0.99668 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-17_DPu-I_eb_sed	200
2.9249 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-18_DPu-I_eb_sed	200
12.2578 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-19_DPu-I_eb_sed	200
9.83227 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-1_DPu-I_eb_sed	200
12.9184 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-1-I_DP_eb_sed	200
32.3654 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-1-LTR_DP_eb_sed	200
31.6094 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-21_DPu-I_eb_sed	200
54.2919 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-22_DPu-I_eb_sed	200
23.0131 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-23_DPu-I_eb_sed	200
14.4621 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-24_DPu-I_eb_sed	200
34509 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-25_DPu-I_eb_sed	200
38.6216 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-26_DPu-I_eb_sed	200
47766 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-27_DPu-I_eb_sed	200
14.5449 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-28_DPu-I_eb_sed	200
12.7186 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-29_DPu-I_eb_sed	200
14.1595 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-2_DPu-I_eb_sed	200
12.2754 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-2-I_DP_eb_sed	200
97.3633 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-2-LTR_DP_eb_sed	200
2.6609 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-30_DPu-I_eb_sed	200
29.2143 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-31_DPu-I_eb_sed	200
37.7193 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-32_DPu-I_eb_sed	200
12.2088 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-33_DPu-I_eb_sed	200
31.8095 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-34_DPu-I_eb_sed	200
36.1444 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-35_DPu-I_eb_sed	200
5.30108 sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-36_DPu-I_eb_sed	200

77.8533	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-37_DPu-I_eb_sed	200
9.82866	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-38_DPu-I_eb_sed	200
6.90234	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-39_DPu-I_eb_sed	200
30.1285	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-3_DPu-I_eb_sed	200
81.4548	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-40_DPu-I_eb_sed	200
15.8261	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-4_DPu-I_eb_sed	200
5.97668	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-5_DPu-I_eb_sed	200
12.8649	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-6_DPu-I_eb_sed	200
8.32555	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-7_DPu-I_eb_sed	200
44.0139	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-8_DPu-I_eb_sed	200
16.0444	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-9_DPu-I_eb_sed	200
56.7801	sex	Gypsy	Daphnia	Dpu_eb1	Gypsy-N1_DPu-I_eb_sed	200
67.9904	sex	L2	Daphnia	Dpu_eb1	L2-1_DPu_eb_sed	200
511535	sex	LT1	Daphnia	Dpu_eb1	LT1_DPu-I_eb_sed	200
7.82747	sex	LT2	Daphnia	Dpu_eb1	LT2_DPu-I_eb_sed	200
45.4296	sex	Mariner	Daphnia	Dpu_eb1	Mariner-1_DPu_eb_sed	200
10.5131	sex	MuDR	Daphnia	Dpu_eb1	MuDR-1_DPu_eb_sed	200
17.1461	sex	MuDRF	Daphnia	Dpu_eb1	MuDRF-1_DPu_eb_sed	200
22048	sex	Nimb	Daphnia	Dpu_eb1	Nimb-1_DPu_eb_sed	200
28131	sex	P	Daphnia	Dpu_eb1	P-1_DPu_eb_sed	200
111445	sex	piggyBac	Daphnia	Dpu_eb1	piggyBac-1_DPu_eb_sed	200
145037	sex	POKEY	Daphnia	Dpu_eb1	POKEY_DP_eb_sed	200
4.45932	sex	Sola1	Daphnia	Dpu_eb1	Sola1-1_DPu_eb_sed	200
4.29095	sex	Sola2	Daphnia	Dpu_eb1	Sola2-1_DPu_eb_sed	200
12.3519	sex	Sola2	Daphnia	Dpu_eb1	Sola2-2_DPu_eb_sed	200
47.7546	sex	Sola2	Daphnia	Dpu_eb1	Sola2-3_DPu_eb_sed	200
8.49652	sex	Sola3	Daphnia	Dpu_eb1	Sola3-1_DPu_eb_sed	200
273248	sex	Tx1	Daphnia	Dpu_eb1	Tx1-1_DPu_eb_sed	200
1.66638	sex	Zator	Daphnia	Dpu_eb1	Zator-1_DPu_eb_sed	200
19.0961	sex	Academ	Daphnia	Dpu_lpb86	Academ-1_DPu_lpb_5w	200
18.9029	sex	BEL	Daphnia	Dpu_lpb86	BEL-10_DPu-I_lpb_5w	200
61.2687	sex	BEL	Daphnia	Dpu_lpb86	BEL-11_DPu-I_lpb_5w	200
46794	sex	BEL	Daphnia	Dpu_lpb86	BEL-12_DPu-I_lpb_5w	200
4.35849	sex	BEL	Daphnia	Dpu_lpb86	BEL-13_DPu-I_lpb_5w	200
45281	sex	BEL	Daphnia	Dpu_lpb86	BEL-14_DPu-I_lpb_5w	200
15.2141	sex	BEL	Daphnia	Dpu_lpb86	BEL-15_DPu-I_lpb_5w	200
16.1767	sex	BEL	Daphnia	Dpu_lpb86	BEL-16_DPu-I_lpb_5w	200
21.3473	sex	BEL	Daphnia	Dpu_lpb86	BEL-17_DPu-I_lpb_5w	200
24.2344	sex	BEL	Daphnia	Dpu_lpb86	BEL-18_DPu-I_lpb_5w	200
8.54971	sex	BEL	Daphnia	Dpu_lpb86	BEL-19_DPu-I_lpb_5w	200
7.04662	sex	BEL	Daphnia	Dpu_lpb86	BEL-1_DPu-I_lpb_5w	200
9.39948	sex	BEL	Daphnia	Dpu_lpb86	BEL-2_DPu-I_lpb_5w	200
25.7248	sex	BEL	Daphnia	Dpu_lpb86	BEL-3_DPu-I_lpb_5w	200
60.7187	sex	BEL	Daphnia	Dpu_lpb86	BEL-4_DPu-I_lpb_5w	200
11.8524	sex	BEL	Daphnia	Dpu_lpb86	BEL-5_DPu-I_lpb_5w	200
5.47229	sex	BEL	Daphnia	Dpu_lpb86	BEL-6_DPu-I_lpb_5w	200
11.3885	sex	BEL	Daphnia	Dpu_lpb86	BEL-7_DPu-I_lpb_5w	200
27.7988	sex	BEL	Daphnia	Dpu_lpb86	BEL-8_DPu-I_lpb_5w	200
34.4807	sex	BEL-9	Daphnia	Dpu_lpb86	BEL-9_DPu_lpb_5w	200
12.9275	sex	Copia	Daphnia	Dpu_lpb86	Copia-10_DPu-I_lpb_5w	200
10.2322	sex	Copia	Daphnia	Dpu_lpb86	Copia-11_DPu-I_lpb_5w	200
4.6777	sex	Copia	Daphnia	Dpu_lpb86	Copia-12_DPu-I_lpb_5w	200
21.8512	sex	Copia	Daphnia	Dpu_lpb86	Copia-13_DPu-I_lpb_5w	200
24.7437	sex	Copia	Daphnia	Dpu_lpb86	Copia-14_DPu-I_lpb_5w	200
12.1327	sex	Copia	Daphnia	Dpu_lpb86	Copia-15_DPu-I_lpb_5w	200
14.9028	sex	Copia	Daphnia	Dpu_lpb86	Copia-16_DPu-I_lpb_5w	200
30.0776	sex	Copia	Daphnia	Dpu_lpb86	Copia-17_DPu-I_lpb_5w	200
13.9799	sex	Copia	Daphnia	Dpu_lpb86	Copia-18_DPu-I_lpb_5w	200
5.91971	sex	Copia	Daphnia	Dpu_lpb86	Copia-19_DPu-I_lpb_5w	200
6.96579	sex	Copia	Daphnia	Dpu_lpb86	Copia-1_DPu-I_lpb_5w	200

10.3424	sex	Copia	Daphnia	Dpu_lpb86	Copia-20_DPu-I_lpb_5w	200
17.3256	sex	Copia	Daphnia	Dpu_lpb86	Copia-21_DPu-I_lpb_5w	200
10249	sex	Copia	Daphnia	Dpu_lpb86	Copia-22_DPu-I_lpb_5w	200
10.5569	sex	Copia	Daphnia	Dpu_lpb86	Copia-23_DPu-I_lpb_5w	200
7.44243	sex	Copia	Daphnia	Dpu_lpb86	Copia-24_DPu-I_lpb_5w	200
36.0343	sex	Copia	Daphnia	Dpu_lpb86	Copia-25_DPu-I_lpb_5w	200
10.7776	sex	Copia	Daphnia	Dpu_lpb86	Copia-26_DPu-I_lpb_5w	200
30.1713	sex	Copia	Daphnia	Dpu_lpb86	Copia-27_DPu-I_lpb_5w	200
16.5387	sex	Copia	Daphnia	Dpu_lpb86	Copia-28_DPu-I_lpb_5w	200
37.9407	sex	Copia	Daphnia	Dpu_lpb86	Copia-29_DPu-I_lpb_5w	200
13.2231	sex	Copia	Daphnia	Dpu_lpb86	Copia-2_DPu-I_lpb_5w	200
4.86172	sex	Copia	Daphnia	Dpu_lpb86	Copia-30_DPu-I_lpb_5w	200
10.3676	sex	Copia	Daphnia	Dpu_lpb86	Copia-31_DPu-I_lpb_5w	200
16.6383	sex	Copia	Daphnia	Dpu_lpb86	Copia-32_DPu-I_lpb_5w	200
2.69813	sex	Copia	Daphnia	Dpu_lpb86	Copia-33_DPu-I_lpb_5w	200
19.3541	sex	Copia	Daphnia	Dpu_lpb86	Copia-34_DPu-I_lpb_5w	200
24.2611	sex	Copia	Daphnia	Dpu_lpb86	Copia-35_DPu-I_lpb_5w	200
5.73575	sex	Copia	Daphnia	Dpu_lpb86	Copia-36_DPu-I_lpb_5w	200
17.1177	sex	Copia	Daphnia	Dpu_lpb86	Copia-37_DPu-I_lpb_5w	200
9.5217	sex	Copia	Daphnia	Dpu_lpb86	Copia-38_DPu-I_lpb_5w	200
12.1658	sex	Copia	Daphnia	Dpu_lpb86	Copia-39_DPu-I_lpb_5w	200
1.13425	sex	Copia	Daphnia	Dpu_lpb86	Copia-3_DPu-I_lpb_5w	200
3.2322	sex	Copia	Daphnia	Dpu_lpb86	Copia-4_DPu-I_lpb_5w	200
22.6259	sex	Copia	Daphnia	Dpu_lpb86	Copia-5_DPu-I_lpb_5w	200
2.23755	sex	Copia	Daphnia	Dpu_lpb86	Copia-6_DPu-I_lpb_5w	200
21.0313	sex	Copia	Daphnia	Dpu_lpb86	Copia-7_DPu-I_lpb_5w	200
9.63557	sex	Copia	Daphnia	Dpu_lpb86	Copia-8_DPu-I_lpb_5w	200
8.57173	sex	Copia	Daphnia	Dpu_lpb86	Copia-9_DPu-I_lpb_5w	200
12.5235	sex	DIRS	Daphnia	Dpu_lpb86	DIRS-1_DPu_lpb_5w	200
20.1456	sex	DIRS	Daphnia	Dpu_lpb86	DIRS-2_DPu_lpb_5w	200
8.44379	sex	DIRS	Daphnia	Dpu_lpb86	DIRS-3_DPu_lpb_5w	200
17.9222	sex	DIRS	Daphnia	Dpu_lpb86	DIRS-4_DPu_lpb_5w	200
8.88385	sex	DIRS	Daphnia	Dpu_lpb86	DIRS-5_DPu_lpb_5w	200
23.5371	sex	DIRS	Daphnia	Dpu_lpb86	DIRS-6_DPu_lpb_5w	200
472009	sex	DNA	Daphnia	Dpu_lpb86	DNA-1_DPu_lpb_5w	200
52289	sex	DNA2	Daphnia	Dpu_lpb86	DNA2-1_DPu_lpb_5w	200
681954	sex	DNA	Daphnia	Dpu_lpb86	DNA-2_DPu_lpb_5w	200
51.7963	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-10_DPu-I_lpb_5w	200
45164	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-11_DPu-I_lpb_5w	200
12.5719	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-12_DPu-I_lpb_5w	200
13.9904	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-13_DPu-I_lpb_5w	200
27.8021	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-14_DPu-I_lpb_5w	200
7.15058	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-15_DPu-I_lpb_5w	200
6.77058	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-16_DPu-I_lpb_5w	200
0.821633	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-17_DPu-I_lpb_5w	200
4.23165	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-18_DPu-I_lpb_5w	200
10.2623	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-19_DPu-I_lpb_5w	200
18.1596	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-1_DPu-I_lpb_5w	200
22.5403	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-1-I_DP_lpb_5w	200
63.4699	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-1-LTR_DP_lpb_5w	200
53.2695	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-21_DPu-I_lpb_5w	200
44.6017	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-22_DPu-I_lpb_5w	200
16129	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-23_DPu-I_lpb_5w	200
16.5942	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-24_DPu-I_lpb_5w	200
3.25184	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-25_DPu-I_lpb_5w	200
32.5895	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-26_DPu-I_lpb_5w	200
38.8581	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-27_DPu-I_lpb_5w	200
19.3695	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-28_DPu-I_lpb_5w	200
22.7448	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-29_DPu-I_lpb_5w	200
5.7887	sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-2_DPu-I_lpb_5w	200

13.5972 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-2-I_DP_lpb_5w	200
128.16 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-2-LTR_DP_lpb_5w	200
6.19754 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-30_DPu-I_lpb_5w	200
36.5292 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-31_DPu-I_lpb_5w	200
37.4745 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-32_DPu-I_lpb_5w	200
23805 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-33_DPu-I_lpb_5w	200
26.4573 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-34_DPu-I_lpb_5w	200
39.1277 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-35_DPu-I_lpb_5w	200
11.1893 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-36_DPu-I_lpb_5w	200
83.3246 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-37_DPu-I_lpb_5w	200
12669 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-38_DPu-I_lpb_5w	200
10.3441 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-39_DPu-I_lpb_5w	200
44.83 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-3_DPu-I_lpb_5w	200
74.9645 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-40_DPu-I_lpb_5w	200
10.0393 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-4_DPu-I_lpb_5w	200
5.92667 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-5_DPu-I_lpb_5w	200
16.9171 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-6_DPu-I_lpb_5w	200
11665 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-7_DPu-I_lpb_5w	200
41.1916 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-8_DPu-I_lpb_5w	200
25.7983 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-9_DPu-I_lpb_5w	200
58.6459 sex	Gypsy	Daphnia	Dpu_lpb86	Gypsy-N1_DPu-I_lpb_5w	200
55356 sex	L2	Daphnia	Dpu_lpb86	L2-1_DPu_lpb_5w	200
346607 sex	LT1	Daphnia	Dpu_lpb86	LT1_DPu-I_lpb_5w	200
22.9235 sex	LT2	Daphnia	Dpu_lpb86	LT2_DPu-I_lpb_5w	200
40.6749 sex	Mariner	Daphnia	Dpu_lpb86	Mariner-1_DPu_lpb_5w	200
14.5103 sex	MuDR	Daphnia	Dpu_lpb86	MuDR-1_DPu_lpb_5w	200
12.4441 sex	MuDRF	Daphnia	Dpu_lpb86	MuDRF-1_DPu_lpb_5w	200
9.37687 sex	Nimb	Daphnia	Dpu_lpb86	Nimb-1_DPu_lpb_5w	200
21.3966 sex	P	Daphnia	Dpu_lpb86	P-1_DPu_lpb_5w	200
112077 sex	piggyBac	Daphnia	Dpu_lpb86	piggyBac-1_DPu_lpb_5w	200
123712 sex	POKEY	Daphnia	Dpu_lpb86	POKEY_DP_lpb_5w	200
5.13171 sex	Sola1	Daphnia	Dpu_lpb86	Sola1-1_DPu_lpb_5w	200
7.40378 sex	Sola2	Daphnia	Dpu_lpb86	Sola2-1_DPu_lpb_5w	200
10641 sex	Sola2	Daphnia	Dpu_lpb86	Sola2-2_DPu_lpb_5w	200
48.9672 sex	Sola2	Daphnia	Dpu_lpb86	Sola2-3_DPu_lpb_5w	200
8.91715 sex	Sola3	Daphnia	Dpu_lpb86	Sola3-1_DPu_lpb_5w	200
327372 sex	Tx1	Daphnia	Dpu_lpb86	Tx1-1_DPu_lpb_5w	200
12.3374 sex	Zator	Daphnia	Dpu_lpb86	Zator-1_DPu_lpb_5w	200
28.5137 asex	Academ	Daphnia	Dpu_sed2	Academ-1_DPu_eb_sed	200
13.4337 asex	BEL	Daphnia	Dpu_sed2	BEL-10_DPu-I_eb_sed	200
54.8057 asex	BEL	Daphnia	Dpu_sed2	BEL-11_DPu-I_eb_sed	200
73.0122 asex	BEL	Daphnia	Dpu_sed2	BEL-12_DPu-I_eb_sed	200
4.38494 asex	BEL	Daphnia	Dpu_sed2	BEL-13_DPu-I_eb_sed	200
36.3638 asex	BEL	Daphnia	Dpu_sed2	BEL-14_DPu-I_eb_sed	200
12.4971 asex	BEL	Daphnia	Dpu_sed2	BEL-15_DPu-I_eb_sed	200
24.8626 asex	BEL	Daphnia	Dpu_sed2	BEL-16_DPu-I_eb_sed	200
36.6719 asex	BEL	Daphnia	Dpu_sed2	BEL-17_DPu-I_eb_sed	200
32.1855 asex	BEL	Daphnia	Dpu_sed2	BEL-18_DPu-I_eb_sed	200
29.9211 asex	BEL	Daphnia	Dpu_sed2	BEL-19_DPu-I_eb_sed	200
4.74144 asex	BEL	Daphnia	Dpu_sed2	BEL-1_DPu-I_eb_sed	200
9.30864 asex	BEL	Daphnia	Dpu_sed2	BEL-2_DPu-I_eb_sed	200
29607 asex	BEL	Daphnia	Dpu_sed2	BEL-3_DPu-I_eb_sed	200
49.2473 asex	BEL	Daphnia	Dpu_sed2	BEL-4_DPu-I_eb_sed	200
7.67504 asex	BEL	Daphnia	Dpu_sed2	BEL-5_DPu-I_eb_sed	200
5.42143 asex	BEL	Daphnia	Dpu_sed2	BEL-6_DPu-I_eb_sed	200
18073 asex	BEL	Daphnia	Dpu_sed2	BEL-7_DPu-I_eb_sed	200
35.5957 asex	BEL	Daphnia	Dpu_sed2	BEL-8_DPu-I_eb_sed	200
34.9482 asex	BEL-9	Daphnia	Dpu_sed2	BEL-9_DPu_eb_sed	200
9.26185 asex	Copia	Daphnia	Dpu_sed2	Copia-10_DPu-I_eb_sed	200
6.81077 asex	Copia	Daphnia	Dpu_sed2	Copia-11_DPu-I_eb_sed	200

8.12245	asex	Copia	Daphnia	Dpu_sed2	Copia-12_DPu-I_eb_sed	200
19.0354	asex	Copia	Daphnia	Dpu_sed2	Copia-13_DPu-I_eb_sed	200
36.9512	asex	Copia	Daphnia	Dpu_sed2	Copia-14_DPu-I_eb_sed	200
9.66215	asex	Copia	Daphnia	Dpu_sed2	Copia-15_DPu-I_eb_sed	200
15.1563	asex	Copia	Daphnia	Dpu_sed2	Copia-16_DPu-I_eb_sed	200
23.9306	asex	Copia	Daphnia	Dpu_sed2	Copia-17_DPu-I_eb_sed	200
8.33898	asex	Copia	Daphnia	Dpu_sed2	Copia-18_DPu-I_eb_sed	200
5.4086	asex	Copia	Daphnia	Dpu_sed2	Copia-19_DPu-I_eb_sed	200
8.14059	asex	Copia	Daphnia	Dpu_sed2	Copia-1_DPu-I_eb_sed	200
13.5464	asex	Copia	Daphnia	Dpu_sed2	Copia-20_DPu-I_eb_sed	200
13.5835	asex	Copia	Daphnia	Dpu_sed2	Copia-21_DPu-I_eb_sed	200
10.7395	asex	Copia	Daphnia	Dpu_sed2	Copia-22_DPu-I_eb_sed	200
13.5665	asex	Copia	Daphnia	Dpu_sed2	Copia-23_DPu-I_eb_sed	200
19.4018	asex	Copia	Daphnia	Dpu_sed2	Copia-24_DPu-I_eb_sed	200
29.0327	asex	Copia	Daphnia	Dpu_sed2	Copia-25_DPu-I_eb_sed	200
11.8386	asex	Copia	Daphnia	Dpu_sed2	Copia-26_DPu-I_eb_sed	200
10.4816	asex	Copia	Daphnia	Dpu_sed2	Copia-27_DPu-I_eb_sed	200
14.4813	asex	Copia	Daphnia	Dpu_sed2	Copia-28_DPu-I_eb_sed	200
41.1789	asex	Copia	Daphnia	Dpu_sed2	Copia-29_DPu-I_eb_sed	200
13.06	asex	Copia	Daphnia	Dpu_sed2	Copia-2_DPu-I_eb_sed	200
12.0925	asex	Copia	Daphnia	Dpu_sed2	Copia-30_DPu-I_eb_sed	200
12.5182	asex	Copia	Daphnia	Dpu_sed2	Copia-31_DPu-I_eb_sed	200
12.0163	asex	Copia	Daphnia	Dpu_sed2	Copia-32_DPu-I_eb_sed	200
7.03778	asex	Copia	Daphnia	Dpu_sed2	Copia-33_DPu-I_eb_sed	200
8.16523	asex	Copia	Daphnia	Dpu_sed2	Copia-34_DPu-I_eb_sed	200
23.7508	asex	Copia	Daphnia	Dpu_sed2	Copia-35_DPu-I_eb_sed	200
5.8134	asex	Copia	Daphnia	Dpu_sed2	Copia-36_DPu-I_eb_sed	200
23005	asex	Copia	Daphnia	Dpu_sed2	Copia-37_DPu-I_eb_sed	200
7.13603	asex	Copia	Daphnia	Dpu_sed2	Copia-38_DPu-I_eb_sed	200
13.5486	asex	Copia	Daphnia	Dpu_sed2	Copia-39_DPu-I_eb_sed	200
20.5825	asex	Copia	Daphnia	Dpu_sed2	Copia-3_DPu-I_eb_sed	200
2.14316	asex	Copia	Daphnia	Dpu_sed2	Copia-4_DPu-I_eb_sed	200
13.8153	asex	Copia	Daphnia	Dpu_sed2	Copia-5_DPu-I_eb_sed	200
11.5238	asex	Copia	Daphnia	Dpu_sed2	Copia-6_DPu-I_eb_sed	200
16.1656	asex	Copia	Daphnia	Dpu_sed2	Copia-7_DPu-I_eb_sed	200
16.3553	asex	Copia	Daphnia	Dpu_sed2	Copia-8_DPu-I_eb_sed	200
9.48426	asex	Copia	Daphnia	Dpu_sed2	Copia-9_DPu-I_eb_sed	200
11.4388	asex	DIRS	Daphnia	Dpu_sed2	DIRS-1_DPu_eb_sed	200
17.1891	asex	DIRS	Daphnia	Dpu_sed2	DIRS-2_DPu_eb_sed	200
12.8314	asex	DIRS	Daphnia	Dpu_sed2	DIRS-3_DPu_eb_sed	200
16.5613	asex	DIRS	Daphnia	Dpu_sed2	DIRS-4_DPu_eb_sed	200
10466	asex	DIRS	Daphnia	Dpu_sed2	DIRS-5_DPu_eb_sed	200
15.3028	asex	DIRS	Daphnia	Dpu_sed2	DIRS-6_DPu_eb_sed	200
512858	asex	DNA	Daphnia	Dpu_sed2	DNA-1_DPu_eb_sed	200
60.0853	asex	DNA2	Daphnia	Dpu_sed2	DNA2-1_DPu_eb_sed	200
611307	asex	DNA	Daphnia	Dpu_sed2	DNA-2_DPu_eb_sed	200
52666	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-10_DPu-I_eb_sed	200
22.7143	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-11_DPu-I_eb_sed	200
13072	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-12_DPu-I_eb_sed	200
11.7871	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-13_DPu-I_eb_sed	200
14.3748	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-14_DPu-I_eb_sed	200
15.0943	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-15_DPu-I_eb_sed	200
5.2206	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-16_DPu-I_eb_sed	200
1296	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-17_DPu-I_eb_sed	200
2.2108	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-18_DPu-I_eb_sed	200
12.8582	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-19_DPu-I_eb_sed	200
12.9771	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-1_DPu-I_eb_sed	200
19709	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-1-I_DP_eb_sed	200
42935	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-1-LTR_DP_eb_sed	200
23805	asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-21_DPu-I_eb_sed	200

44.4196 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-22_DPu-I_eb_sed	200
21738 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-23_DPu-I_eb_sed	200
29984 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-24_DPu-I_eb_sed	200
20.9868 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-25_DPu-I_eb_sed	200
40.2346 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-26_DPu-I_eb_sed	200
43.6977 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-27_DPu-I_eb_sed	200
15.2925 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-28_DPu-I_eb_sed	200
14.4749 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-29_DPu-I_eb_sed	200
11.3743 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-2_DPu-I_eb_sed	200
12.0597 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-2-I_DP_eb_sed	200
90.7597 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-2-LTR_DP_eb_sed	200
14994 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-30_DPu-I_eb_sed	200
30.3136 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-31_DPu-I_eb_sed	200
56.3163 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-32_DPu-I_eb_sed	200
11.8044 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-33_DPu-I_eb_sed	200
26.1592 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-34_DPu-I_eb_sed	200
58.3227 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-35_DPu-I_eb_sed	200
16.7465 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-36_DPu-I_eb_sed	200
113076 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-37_DPu-I_eb_sed	200
9.65515 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-38_DPu-I_eb_sed	200
9.2348 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-39_DPu-I_eb_sed	200
38.9071 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-3_DPu-I_eb_sed	200
84.0277 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-40_DPu-I_eb_sed	200
14.1042 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-4_DPu-I_eb_sed	200
7.16283 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-5_DPu-I_eb_sed	200
16.3199 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-6_DPu-I_eb_sed	200
14.6521 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-7_DPu-I_eb_sed	200
37.6048 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-8_DPu-I_eb_sed	200
24.9082 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-9_DPu-I_eb_sed	200
23053 asex	Gypsy	Daphnia	Dpu_sed2	Gypsy-N1_DPu-I_eb_sed	200
83.5492 asex	L2	Daphnia	Dpu_sed2	L2-1_DPu_eb_sed	200
405.19 asex	LT1	Daphnia	Dpu_sed2	LT1_DPu-I_eb_sed	200
24.4326 asex	LT2	Daphnia	Dpu_sed2	LT2_DPu-I_eb_sed	200
49.9978 asex	Mariner	Daphnia	Dpu_sed2	Mariner-1_DPu_eb_sed	200
18.8379 asex	MuDR	Daphnia	Dpu_sed2	MuDR-1_DPu_eb_sed	200
9.94302 asex	MuDRF	Daphnia	Dpu_sed2	MuDRF-1_DPu_eb_sed	200
17.8033 asex	Nimb	Daphnia	Dpu_sed2	Nimb-1_DPu_eb_sed	200
28.3921 asex	P	Daphnia	Dpu_sed2	P-1_DPu_eb_sed	200
105648 asex	piggyBac	Daphnia	Dpu_sed2	piggyBac-1_DPu_eb_sed	200
135391 asex	POKEY	Daphnia	Dpu_sed2	POKEY_DP_eb_sed	200
4.25673 asex	Sola1	Daphnia	Dpu_sed2	Sola1-1_DPu_eb_sed	200
14.2901 asex	Sola2	Daphnia	Dpu_sed2	Sola2-1_DPu_eb_sed	200
6.57222 asex	Sola2	Daphnia	Dpu_sed2	Sola2-2_DPu_eb_sed	200
49.9577 asex	Sola2	Daphnia	Dpu_sed2	Sola2-3_DPu_eb_sed	200
9.65686 asex	Sola3	Daphnia	Dpu_sed2	Sola3-1_DPu_eb_sed	200
304284 asex	Tx1	Daphnia	Dpu_sed2	Tx1-1_DPu_eb_sed	200
17.8141 asex	Zator	Daphnia	Dpu_sed2	Zator-1_DPu_eb_sed	200
4.3093 asex	BEL	Lclav	Lc_asex	BEL-1--LTR/BEL_Lc	320
406673 asex	BEL	Lclav	Lc_asex	BEL-2--LTR/BEL_Lc	320
275334 asex	BEL	Lclav	Lc_asex	BEL-3--LTR/BEL_Lc	320
23.6721 asex	BEL	Lclav	Lc_asex	BEL-4--LTR/BEL_Lc	320
326392 asex	BEL	Lclav	Lc_asex	BEL-5--LTR/BEL_Lc	320
127919 asex	Chapaev	Lclav	Lc_asex	Chapaev-1--DNA/Transib_Lc	320
14772.4 asex	Chapaev	Lclav	Lc_asex	Chapaev-2--DNA/Transib_Lc	320
150208 asex	Chapaev	Lclav	Lc_asex	Chapaev-3--DNA/Transib_Lc	320
379844 asex	Chapaev	Lclav	Lc_asex	Chapaev-4--DNA/Transib_Lc	320
883.43 asex	Chapaev	Lclav	Lc_asex	Chapaev-5--DNA/Transib_Lc	320
208784 asex	Chapaev	Lclav	Lc_asex	Chapaev-6--DNA/Transib_Lc	320
211289 asex	Chapaev	Lclav	Lc_asex	Chapaev-7--DNA/Transib_Lc	320
16.1576 asex	Copia	Lclav	Lc_asex	Copia-1--LTR/Copia_Lc	320

7.01438	asex	Copia	Lclav	Lc_asex	Copia-2--LTR/Copia_Lc	320
30144	asex	Copia	Lclav	Lc_asex	Copia-3--LTR/Copia_Lc	320
13.0024	asex	Copia	Lclav	Lc_asex	Copia-4--LTR/Copia_Lc	320
9.43003	asex	Copia	Lclav	Lc_asex	Copia-5--LTR/Copia_Lc	320
32.4966	asex	Copia	Lclav	Lc_asex	Copia-6--LTR/Copia_Lc	320
2.73854	asex	CR1	Lclav	Lc_asex	CR1-1--LINE/CR1_Lc	320
3.26859	asex	CR1	Lclav	Lc_asex	CR1-2--LINE/CR1_Lc	320
12.4629	asex	Crypton	Lclav	Lc_asex	Crypton-1--DNA/Crypton_Lc	320
4.0325	asex	DIRS	Lclav	Lc_asex	DIRS-1--LTR/DIRS_Lc	320
15.3587	asex	DIRS	Lclav	Lc_asex	DIRS-2--LTR/DIRS_Lc	320
10.2458	asex	DIRS	Lclav	Lc_asex	DIRS-3--LTR/DIRS_Lc	320
17.6777	asex	EnSpm	Lclav	Lc_asex	EnSpm-1--DNA/EnSpm_Lc	320
321575	asex	EnSpm	Lclav	Lc_asex	EnSpm-2--DNA/EnSpm_Lc	320
6.86945	asex	EnSpm_HAT	Lclav	Lc_asex	EnSpm_HAT-1--DNA/EnSpm_Lc	320
35.6415	asex	Ginger	Lclav	Lc_asex	Ginger-1--DNA/Ginger_Lc	320
146602	asex	Gypsy	Lclav	Lc_asex	Gypsy-10--LTR/Gypsy_Lc	320
174289	asex	Gypsy	Lclav	Lc_asex	Gypsy-11--LTR/Gypsy_Lc	320
435152	asex	Gypsy	Lclav	Lc_asex	Gypsy-12--LTR/Gypsy_Lc	320
119587	asex	Gypsy	Lclav	Lc_asex	Gypsy-13--LTR/Gypsy_Lc	320
69.4322	asex	Gypsy	Lclav	Lc_asex	Gypsy-14--LTR/Gypsy_Lc	320
308919	asex	Gypsy	Lclav	Lc_asex	Gypsy-15--LTR/Gypsy_Lc	320
29.5056	asex	Gypsy	Lclav	Lc_asex	Gypsy-16--LTR/Gypsy_Lc	320
223753	asex	Gypsy	Lclav	Lc_asex	Gypsy-17--LTR/Gypsy_Lc	320
159554	asex	Gypsy	Lclav	Lc_asex	Gypsy-18--LTR/Gypsy_Lc	320
79.1178	asex	Gypsy	Lclav	Lc_asex	Gypsy-19--LTR/Gypsy_Lc	320
137058	asex	Gypsy	Lclav	Lc_asex	Gypsy-1--LTR/Gypsy_Lc	320
48.9362	asex	Gypsy	Lclav	Lc_asex	Gypsy-20--LTR/Gypsy_Lc	320
169519	asex	Gypsy	Lclav	Lc_asex	Gypsy-21--LTR/Gypsy_Lc	320
137451	asex	Gypsy	Lclav	Lc_asex	Gypsy-22--LTR/Gypsy_Lc	320
206265	asex	Gypsy	Lclav	Lc_asex	Gypsy-23--LTR/Gypsy_Lc	320
9.22876	asex	Gypsy	Lclav	Lc_asex	Gypsy-24--LTR/Gypsy_Lc	320
91.5569	asex	Gypsy	Lclav	Lc_asex	Gypsy-25--LTR/Gypsy_Lc	320
9.97119	asex	Gypsy	Lclav	Lc_asex	Gypsy-26--LTR/Gypsy_Lc	320
10.4949	asex	Gypsy	Lclav	Lc_asex	Gypsy-27--LTR/Gypsy_Lc	320
17.7856	asex	Gypsy	Lclav	Lc_asex	Gypsy-28--LTR/Gypsy_Lc	320
80.8199	asex	Gypsy	Lclav	Lc_asex	Gypsy-29--LTR/Gypsy_Lc	320
90.5378	asex	Gypsy	Lclav	Lc_asex	Gypsy-2--LTR/Gypsy_Lc	320
145049	asex	Gypsy	Lclav	Lc_asex	Gypsy-30--LTR/Gypsy_Lc	320
120055	asex	Gypsy	Lclav	Lc_asex	Gypsy-31--LTR/Gypsy_Lc	320
219202	asex	Gypsy	Lclav	Lc_asex	Gypsy-32--LTR/Gypsy_Lc	320
153512	asex	Gypsy	Lclav	Lc_asex	Gypsy-33--LTR/Gypsy_Lc	320
21.0231	asex	Gypsy	Lclav	Lc_asex	Gypsy-34--LTR/Gypsy_Lc	320
91241	asex	Gypsy	Lclav	Lc_asex	Gypsy-35--LTR/Gypsy_Lc	320
179114	asex	Gypsy	Lclav	Lc_asex	Gypsy-36--LTR/Gypsy_Lc	320
17615	asex	Gypsy	Lclav	Lc_asex	Gypsy-37--LTR/Gypsy_Lc	320
47.3433	asex	Gypsy	Lclav	Lc_asex	Gypsy-38--LTR/Gypsy_Lc	320
86.0312	asex	Gypsy	Lclav	Lc_asex	Gypsy-39--LTR/Gypsy_Lc	320
111102	asex	Gypsy	Lclav	Lc_asex	Gypsy-3--LTR/Gypsy_Lc	320
23.4255	asex	Gypsy	Lclav	Lc_asex	Gypsy-40--LTR/Gypsy_Lc	320
129529	asex	Gypsy	Lclav	Lc_asex	Gypsy-41--LTR/Gypsy_Lc	320
116174	asex	Gypsy	Lclav	Lc_asex	Gypsy-42--LTR/Gypsy_Lc	320
124617	asex	Gypsy	Lclav	Lc_asex	Gypsy-43--LTR/Gypsy_Lc	320
211.56	asex	Gypsy	Lclav	Lc_asex	Gypsy-44--LTR/Gypsy_Lc	320
52.0482	asex	Gypsy	Lclav	Lc_asex	Gypsy-45--LTR/Gypsy_Lc	320
162694	asex	Gypsy	Lclav	Lc_asex	Gypsy-46--LTR/Gypsy_Lc	320
32.9768	asex	Gypsy	Lclav	Lc_asex	Gypsy-47--LTR/Gypsy_Lc	320
64.4757	asex	Gypsy	Lclav	Lc_asex	Gypsy-48--LTR/Gypsy_Lc	320
264075	asex	Gypsy	Lclav	Lc_asex	Gypsy-49--LTR/Gypsy_Lc	320
6.7687	asex	Gypsy	Lclav	Lc_asex	Gypsy-4--LTR/Gypsy_Lc	320
31.9191	asex	Gypsy	Lclav	Lc_asex	Gypsy-50--LTR/Gypsy_Lc	320

104377 asex	Gypsy	Lclav	Lc_asex	Gypsy-51--LTR/Gypsy_Lc	320
136567 asex	Gypsy	Lclav	Lc_asex	Gypsy-52--LTR/Gypsy_Lc	320
207131 asex	Gypsy	Lclav	Lc_asex	Gypsy-53--LTR/Gypsy_Lc	320
14.7519 asex	Gypsy	Lclav	Lc_asex	Gypsy-54--LTR/Gypsy_Lc	320
183.43 asex	Gypsy	Lclav	Lc_asex	Gypsy-55--LTR/Gypsy_Lc	320
116198 asex	Gypsy	Lclav	Lc_asex	Gypsy-56--LTR/Gypsy_Lc	320
26.0139 asex	Gypsy	Lclav	Lc_asex	Gypsy-5--LTR/Gypsy_Lc	320
219546 asex	Gypsy	Lclav	Lc_asex	Gypsy-6--LTR/Gypsy_Lc	320
141274 asex	Gypsy	Lclav	Lc_asex	Gypsy-7--LTR/Gypsy_Lc	320
296695 asex	Gypsy	Lclav	Lc_asex	Gypsy-8--LTR/Gypsy_Lc	320
24.8348 asex	Gypsy	Lclav	Lc_asex	Gypsy-9--LTR/Gypsy_Lc	320
15.2453 asex	HAT	Lclav	Lc_asex	HAT-1--DNA/hAT_Lc	320
16.6962 asex	Helitron	Lclav	Lc_asex	Helitron-10--DNA/Helitron_Lc	320
39.7283 asex	Helitron	Lclav	Lc_asex	Helitron-11--DNA/Helitron_Lc	320
7.74274 asex	Helitron	Lclav	Lc_asex	Helitron-12--DNA/Helitron_Lc	320
26.8741 asex	Helitron	Lclav	Lc_asex	Helitron-1--DNA/Helitron_Lc	320
31.2125 asex	Helitron	Lclav	Lc_asex	Helitron-2--DNA/Helitron_Lc	320
133036 asex	Helitron	Lclav	Lc_asex	Helitron-3--DNA/Helitron_Lc	320
569.68 asex	Helitron	Lclav	Lc_asex	Helitron-4--DNA/Helitron_Lc	320
15.7235 asex	Helitron	Lclav	Lc_asex	Helitron-5--DNA/Helitron_Lc	320
49.6432 asex	Helitron	Lclav	Lc_asex	Helitron-6--DNA/Helitron_Lc	320
227.88 asex	Helitron	Lclav	Lc_asex	Helitron-7--DNA/Helitron_Lc	320
1612.86 asex	Helitron	Lclav	Lc_asex	Helitron-8--DNA/Helitron_Lc	320
56525 asex	Helitron	Lclav	Lc_asex	Helitron-9--DNA/Helitron_Lc	320
8.31544 asex	I	Lclav	Lc_asex	I-1--LINE/I_Lc	320
19.0205 asex	I	Lclav	Lc_asex	I-2--LINE/I_Lc	320
52.2531 asex	I	Lclav	Lc_asex	I-3--LINE/I_Lc	320
8.71207 asex	I	Lclav	Lc_asex	I-4--LINE/I_Lc	320
87.9356 asex	I	Lclav	Lc_asex	I-5--LINE/I_Lc	320
9.05269 asex	Jockey	Lclav	Lc_asex	Jockey-1--LINE/Jockey_Lc	320
68.2406 asex	Kolobok	Lclav	Lc_asex	Kolobok-1--DNA/Kolobok_Lc	320
220386 asex	Kolobok	Lclav	Lc_asex	Kolobok-2--DNA/Kolobok_Lc	320
324874 asex	Kolobok	Lclav	Lc_asex	Kolobok-3--DNA/Kolobok_Lc	320
73.3303 asex	Kolobok	Lclav	Lc_asex	Kolobok-4--DNA/Kolobok_Lc	320
32.0533 asex	Kolobok	Lclav	Lc_asex	Kolobok-5--DNA/Kolobok_Lc	320
59.1745 asex	L2	Lclav	Lc_asex	L2-1--LINE/L2_Lc	320
7.3804 asex	L2	Lclav	Lc_asex	L2-2--LINE/L2_Lc	320
739.12 asex	Loa	Lclav	Lc_asex	Loa-1--LINE/Loa_Lc	320
321913 asex	Loa	Lclav	Lc_asex	Loa-2--LINE/Loa_Lc	320
44.2667 asex	Loa	Lclav	Lc_asex	Loa-3--LINE/Loa_Lc	320
146979 asex	Loa	Lclav	Lc_asex	Loa-4--LINE/Loa_Lc	320
682071 asex	Loa	Lclav	Lc_asex	Loa-5--LINE/Loa_Lc	320
90.2967 asex	Loa	Lclav	Lc_asex	Loa-6--LINE/Loa_Lc	320
68.9907 asex	Loa	Lclav	Lc_asex	Loa-7--LINE/Loa_Lc	320
53.1338 asex	LTR	Lclav	Lc_asex	LTR-1--LTR/LTR_Lc	320
10.8422 asex	LTR	Lclav	Lc_asex	LTR-2--LTR/LTR_Lc	320
17.6606 asex	MuDR	Lclav	Lc_asex	MuDR-1--DNA/MuDr_Lc	320
7.25974 asex	MuDR	Lclav	Lc_asex	MuDR-2--DNA/MuDr_Lc	320
11.3957 asex	MuDR	Lclav	Lc_asex	MuDR-3--DNA/MuDr_Lc	320
6.2848 asex	NONLTR	Lclav	Lc_asex	NONLTR-1--LINE/LINE_Lc	320
34.5057 asex	Penelope	Lclav	Lc_asex	Penelope-1--LINE/Penelope_Lc	320
4.03347 asex	Penelope	Lclav	Lc_asex	Penelope-2--LINE/Penelope_Lc	320
8.34646 asex	Penelope	Lclav	Lc_asex	Penelope-3--LINE/Penelope_Lc	320
10.8018 asex	Penelope	Lclav	Lc_asex	Penelope-4--LINE/Penelope_Lc	320
74.3215 asex	PiggyBac	Lclav	Lc_asex	PiggyBac-1--DNA/PiggyBac_Lc	320
87.3731 asex	PiggyBac	Lclav	Lc_asex	PiggyBac-2--DNA/PiggyBac_Lc	320
453842 asex	PiggyBac	Lclav	Lc_asex	PiggyBac-3--DNA/PiggyBac_Lc	320
36.7361 asex	Polinton	Lclav	Lc_asex	Polinton-1--DNA/Polinton_Lc	320
79.4975 asex	Polinton	Lclav	Lc_asex	Polinton-2--DNA/Polinton_Lc	320
108519 asex	Polinton	Lclav	Lc_asex	Polinton-3--DNA/Polinton_Lc	320

61.5228	asex	Polinton	Lclav	Lc_asex	Polinton-4--DNA/Polinton_Lc	320
81.2031	asex	Polinton	Lclav	Lc_asex	Polinton-5--DNA/Polinton_Lc	320
76.0171	asex	Polinton	Lclav	Lc_asex	Polinton-6--DNA/Polinton_Lc	320
123136	asex	Polinton	Lclav	Lc_asex	Polinton-7--DNA/Polinton_Lc	320
110234	asex	Polinton	Lclav	Lc_asex	Polinton-8--DNA/Polinton_Lc	320
3615.79	asex	R1	Lclav	Lc_asex	R1-1--LINE/R1_Lc	320
780605	asex	R1	Lclav	Lc_asex	R1-2--LINE/R1_Lc	320
942.73	asex	R1	Lclav	Lc_asex	R1-3--LINE/R1_Lc	320
1425.99	asex	R1	Lclav	Lc_asex	R1-4--LINE/R1_Lc	320
951188	asex	R1	Lclav	Lc_asex	R1-5--LINE/R1_Lc	320
1023.64	asex	R1	Lclav	Lc_asex	R1-6--LINE/R1_Lc	320
7.76375	asex	R1	Lclav	Lc_asex	R1-7--LINE/R1_Lc	320
17.2597	asex	R1	Lclav	Lc_asex	R1-8--LINE/R1_Lc	320
9.94126	asex	RTE	Lclav	Lc_asex	RTE-1--LINE/RTE_Lc	320
6.33974	asex	RTE	Lclav	Lc_asex	RTE-2--LINE/RTE_Lc	320
3.45559	asex	RTE	Lclav	Lc_asex	RTE-3--LINE/RTE_Lc	320
174.18	asex	RTE	Lclav	Lc_asex	RTE-4--LINE/RTE_Lc	320
14958	asex	Sola	Lclav	Lc_asex	Sola-1--DNA/Sola_Lc	320
63.4842	asex	Sola	Lclav	Lc_asex	Sola-2--DNA/Sola_Lc	320
140276	asex	Sola	Lclav	Lc_asex	Sola-3--DNA/Sola_Lc	320
788052	asex	Sola	Lclav	Lc_asex	Sola-4--DNA/Sola_Lc	320
5.14127	asex	Sola	Lclav	Lc_asex	Sola-5--DNA/Sola_Lc	320
9.96297	asex	Sola	Lclav	Lc_asex	Sola-6--DNA/Sola_Lc	320
13.9627	asex	TcMar	Lclav	Lc_asex	TcMar-1--DNA/TcMar_Lc	320
35.1249	asex	TcMar	Lclav	Lc_asex	TcMar-2--DNA/TcMar_Lc	320
1118.51	asex	TcMar	Lclav	Lc_asex	TcMar-3--DNA/TcMar_Lc	320
343053	asex	TcMar_Chapaev	Lclav	Lc_asex	TcMar_Chapaev-1--DNA/TcMar_Lc	320
366733	asex	Transib	Lclav	Lc_asex	Transib-1--DNA/Transib_Lc	320
957551	asex	Transib	Lclav	Lc_asex	Transib-2--DNA/Transib_Lc	320
5.16514	sex	BEL	Lclav	Lc_sex	BEL-1--LTR/BEL_Lc	320
448801	sex	BEL	Lclav	Lc_sex	BEL-2--LTR/BEL_Lc	320
285323	sex	BEL	Lclav	Lc_sex	BEL-3--LTR/BEL_Lc	320
23.8832	sex	BEL	Lclav	Lc_sex	BEL-4--LTR/BEL_Lc	320
349381	sex	BEL	Lclav	Lc_sex	BEL-5--LTR/BEL_Lc	320
136163	sex	Chapaev	Lclav	Lc_sex	Chapaev-1--DNA/Transib_Lc	320
17530.7	sex	Chapaev	Lclav	Lc_sex	Chapaev-2--DNA/Transib_Lc	320
156171	sex	Chapaev	Lclav	Lc_sex	Chapaev-3--DNA/Transib_Lc	320
454174	sex	Chapaev	Lclav	Lc_sex	Chapaev-4--DNA/Transib_Lc	320
1054.59	sex	Chapaev	Lclav	Lc_sex	Chapaev-5--DNA/Transib_Lc	320
212887	sex	Chapaev	Lclav	Lc_sex	Chapaev-6--DNA/Transib_Lc	320
220051	sex	Chapaev	Lclav	Lc_sex	Chapaev-7--DNA/Transib_Lc	320
17.6929	sex	Copia	Lclav	Lc_sex	Copia-1--LTR/Copia_Lc	320
7.99199	sex	Copia	Lclav	Lc_sex	Copia-2--LTR/Copia_Lc	320
16.9009	sex	Copia	Lclav	Lc_sex	Copia-3--LTR/Copia_Lc	320
12.6978	sex	Copia	Lclav	Lc_sex	Copia-4--LTR/Copia_Lc	320
10.2361	sex	Copia	Lclav	Lc_sex	Copia-5--LTR/Copia_Lc	320
23.5444	sex	Copia	Lclav	Lc_sex	Copia-6--LTR/Copia_Lc	320
3.12993	sex	CR1	Lclav	Lc_sex	CR1-1--LINE/CR1_Lc	320
2.3009	sex	CR1	Lclav	Lc_sex	CR1-2--LINE/CR1_Lc	320
9.95607	sex	Crypton	Lclav	Lc_sex	Crypton-1--DNA/Crypton_Lc	320
4.33788	sex	DIRS	Lclav	Lc_sex	DIRS-1--LTR/DIRS_Lc	320
16.1119	sex	DIRS	Lclav	Lc_sex	DIRS-2--LTR/DIRS_Lc	320
7.94331	sex	DIRS	Lclav	Lc_sex	DIRS-3--LTR/DIRS_Lc	320
19.1225	sex	EnSpm	Lclav	Lc_sex	EnSpm-1--DNA/EnSpm_Lc	320
313524	sex	EnSpm	Lclav	Lc_sex	EnSpm-2--DNA/EnSpm_Lc	320
7.29471	sex	EnSpm_HAT	Lclav	Lc_sex	EnSpm_HAT-1--DNA/EnSpm_Lc	320
36.9938	sex	Ginger	Lclav	Lc_sex	Ginger-1--DNA/Ginger_Lc	320
158794	sex	Gypsy	Lclav	Lc_sex	Gypsy-10--LTR/Gypsy_Lc	320
171199	sex	Gypsy	Lclav	Lc_sex	Gypsy-11--LTR/Gypsy_Lc	320
549.16	sex	Gypsy	Lclav	Lc_sex	Gypsy-12--LTR/Gypsy_Lc	320

120436 sex	Gypsy	Lclav	Lc_sex	Gypsy-13--LTR/Gypsy_Lc	320
34.2997 sex	Gypsy	Lclav	Lc_sex	Gypsy-14--LTR/Gypsy_Lc	320
361481 sex	Gypsy	Lclav	Lc_sex	Gypsy-15--LTR/Gypsy_Lc	320
29.5335 sex	Gypsy	Lclav	Lc_sex	Gypsy-16--LTR/Gypsy_Lc	320
114222 sex	Gypsy	Lclav	Lc_sex	Gypsy-17--LTR/Gypsy_Lc	320
189.88 sex	Gypsy	Lclav	Lc_sex	Gypsy-18--LTR/Gypsy_Lc	320
68.6968 sex	Gypsy	Lclav	Lc_sex	Gypsy-19--LTR/Gypsy_Lc	320
157231 sex	Gypsy	Lclav	Lc_sex	Gypsy-1--LTR/Gypsy_Lc	320
41.5971 sex	Gypsy	Lclav	Lc_sex	Gypsy-20--LTR/Gypsy_Lc	320
192294 sex	Gypsy	Lclav	Lc_sex	Gypsy-21--LTR/Gypsy_Lc	320
135297 sex	Gypsy	Lclav	Lc_sex	Gypsy-22--LTR/Gypsy_Lc	320
253594 sex	Gypsy	Lclav	Lc_sex	Gypsy-23--LTR/Gypsy_Lc	320
9.03572 sex	Gypsy	Lclav	Lc_sex	Gypsy-24--LTR/Gypsy_Lc	320
100705 sex	Gypsy	Lclav	Lc_sex	Gypsy-25--LTR/Gypsy_Lc	320
9.84637 sex	Gypsy	Lclav	Lc_sex	Gypsy-26--LTR/Gypsy_Lc	320
9.53243 sex	Gypsy	Lclav	Lc_sex	Gypsy-27--LTR/Gypsy_Lc	320
15.1734 sex	Gypsy	Lclav	Lc_sex	Gypsy-28--LTR/Gypsy_Lc	320
93.2017 sex	Gypsy	Lclav	Lc_sex	Gypsy-29--LTR/Gypsy_Lc	320
111887 sex	Gypsy	Lclav	Lc_sex	Gypsy-2--LTR/Gypsy_Lc	320
176959 sex	Gypsy	Lclav	Lc_sex	Gypsy-30--LTR/Gypsy_Lc	320
112911 sex	Gypsy	Lclav	Lc_sex	Gypsy-31--LTR/Gypsy_Lc	320
230878 sex	Gypsy	Lclav	Lc_sex	Gypsy-32--LTR/Gypsy_Lc	320
83.3626 sex	Gypsy	Lclav	Lc_sex	Gypsy-33--LTR/Gypsy_Lc	320
25.6109 sex	Gypsy	Lclav	Lc_sex	Gypsy-34--LTR/Gypsy_Lc	320
102751 sex	Gypsy	Lclav	Lc_sex	Gypsy-35--LTR/Gypsy_Lc	320
184324 sex	Gypsy	Lclav	Lc_sex	Gypsy-36--LTR/Gypsy_Lc	320
18.8426 sex	Gypsy	Lclav	Lc_sex	Gypsy-37--LTR/Gypsy_Lc	320
47.0764 sex	Gypsy	Lclav	Lc_sex	Gypsy-38--LTR/Gypsy_Lc	320
92.6227 sex	Gypsy	Lclav	Lc_sex	Gypsy-39--LTR/Gypsy_Lc	320
115.12 sex	Gypsy	Lclav	Lc_sex	Gypsy-3--LTR/Gypsy_Lc	320
23.6614 sex	Gypsy	Lclav	Lc_sex	Gypsy-40--LTR/Gypsy_Lc	320
131217 sex	Gypsy	Lclav	Lc_sex	Gypsy-41--LTR/Gypsy_Lc	320
120126 sex	Gypsy	Lclav	Lc_sex	Gypsy-42--LTR/Gypsy_Lc	320
129684 sex	Gypsy	Lclav	Lc_sex	Gypsy-43--LTR/Gypsy_Lc	320
202869 sex	Gypsy	Lclav	Lc_sex	Gypsy-44--LTR/Gypsy_Lc	320
46233 sex	Gypsy	Lclav	Lc_sex	Gypsy-45--LTR/Gypsy_Lc	320
195074 sex	Gypsy	Lclav	Lc_sex	Gypsy-46--LTR/Gypsy_Lc	320
34.3287 sex	Gypsy	Lclav	Lc_sex	Gypsy-47--LTR/Gypsy_Lc	320
52.2744 sex	Gypsy	Lclav	Lc_sex	Gypsy-48--LTR/Gypsy_Lc	320
305141 sex	Gypsy	Lclav	Lc_sex	Gypsy-49--LTR/Gypsy_Lc	320
6.49429 sex	Gypsy	Lclav	Lc_sex	Gypsy-4--LTR/Gypsy_Lc	320
35.3694 sex	Gypsy	Lclav	Lc_sex	Gypsy-50--LTR/Gypsy_Lc	320
110138 sex	Gypsy	Lclav	Lc_sex	Gypsy-51--LTR/Gypsy_Lc	320
68.2277 sex	Gypsy	Lclav	Lc_sex	Gypsy-52--LTR/Gypsy_Lc	320
216966 sex	Gypsy	Lclav	Lc_sex	Gypsy-53--LTR/Gypsy_Lc	320
13.2792 sex	Gypsy	Lclav	Lc_sex	Gypsy-54--LTR/Gypsy_Lc	320
189882 sex	Gypsy	Lclav	Lc_sex	Gypsy-55--LTR/Gypsy_Lc	320
117164 sex	Gypsy	Lclav	Lc_sex	Gypsy-56--LTR/Gypsy_Lc	320
22.5656 sex	Gypsy	Lclav	Lc_sex	Gypsy-5--LTR/Gypsy_Lc	320
229694 sex	Gypsy	Lclav	Lc_sex	Gypsy-6--LTR/Gypsy_Lc	320
163801 sex	Gypsy	Lclav	Lc_sex	Gypsy-7--LTR/Gypsy_Lc	320
351106 sex	Gypsy	Lclav	Lc_sex	Gypsy-8--LTR/Gypsy_Lc	320
24.8072 sex	Gypsy	Lclav	Lc_sex	Gypsy-9--LTR/Gypsy_Lc	320
19.7004 sex	HAT	Lclav	Lc_sex	HAT-1--DNA/hAT_Lc	320
17.8205 sex	Helitron	Lclav	Lc_sex	Helitron-10--DNA/Helitron_Lc	320
27.2431 sex	Helitron	Lclav	Lc_sex	Helitron-11--DNA/Helitron_Lc	320
6.88874 sex	Helitron	Lclav	Lc_sex	Helitron-12--DNA/Helitron_Lc	320
20301 sex	Helitron	Lclav	Lc_sex	Helitron-1--DNA/Helitron_Lc	320
27.7713 sex	Helitron	Lclav	Lc_sex	Helitron-2--DNA/Helitron_Lc	320
125207 sex	Helitron	Lclav	Lc_sex	Helitron-3--DNA/Helitron_Lc	320

546205 sex	Helitron	Lclav	Lc_sex	Helitron-4--DNA/Helitron_Lc	320
12.8263 sex	Helitron	Lclav	Lc_sex	Helitron-5--DNA/Helitron_Lc	320
45.8666 sex	Helitron	Lclav	Lc_sex	Helitron-6--DNA/Helitron_Lc	320
200915 sex	Helitron	Lclav	Lc_sex	Helitron-7--DNA/Helitron_Lc	320
1839.95 sex	Helitron	Lclav	Lc_sex	Helitron-8--DNA/Helitron_Lc	320
47.5191 sex	Helitron	Lclav	Lc_sex	Helitron-9--DNA/Helitron_Lc	320
11.3935 sex	I	Lclav	Lc_sex	I-1--LINE/I_Lc	320
20968 sex	I	Lclav	Lc_sex	I-2--LINE/I_Lc	320
27.9683 sex	I	Lclav	Lc_sex	I-3--LINE/I_Lc	320
6.40263 sex	I	Lclav	Lc_sex	I-4--LINE/I_Lc	320
70.8213 sex	I	Lclav	Lc_sex	I-5--LINE/I_Lc	320
8.61755 sex	Jockey	Lclav	Lc_sex	Jockey-1--LINE/Jockey_Lc	320
59513 sex	Kolobok	Lclav	Lc_sex	Kolobok-1--DNA/Kolobok_Lc	320
187.24 sex	Kolobok	Lclav	Lc_sex	Kolobok-2--DNA/Kolobok_Lc	320
354367 sex	Kolobok	Lclav	Lc_sex	Kolobok-3--DNA/Kolobok_Lc	320
49.4284 sex	Kolobok	Lclav	Lc_sex	Kolobok-4--DNA/Kolobok_Lc	320
33.3481 sex	Kolobok	Lclav	Lc_sex	Kolobok-5--DNA/Kolobok_Lc	320
58777 sex	L2	Lclav	Lc_sex	L2-1--LINE/L2_Lc	320
7.61209 sex	L2	Lclav	Lc_sex	L2-2--LINE/L2_Lc	320
834668 sex	Loa	Lclav	Lc_sex	Loa-1--LINE/Loa_Lc	320
367033 sex	Loa	Lclav	Lc_sex	Loa-2--LINE/Loa_Lc	320
58.1128 sex	Loa	Lclav	Lc_sex	Loa-3--LINE/Loa_Lc	320
171588 sex	Loa	Lclav	Lc_sex	Loa-4--LINE/Loa_Lc	320
751729 sex	Loa	Lclav	Lc_sex	Loa-5--LINE/Loa_Lc	320
108364 sex	Loa	Lclav	Lc_sex	Loa-6--LINE/Loa_Lc	320
95.8624 sex	Loa	Lclav	Lc_sex	Loa-7--LINE/Loa_Lc	320
55.8603 sex	LTR	Lclav	Lc_sex	LTR-1--LTR/LTR_Lc	320
8.89931 sex	LTR	Lclav	Lc_sex	LTR-2--LTR/LTR_Lc	320
11168 sex	MuDR	Lclav	Lc_sex	MuDR-1--DNA/MuDr_Lc	320
7.30744 sex	MuDR	Lclav	Lc_sex	MuDR-2--DNA/MuDr_Lc	320
11.0529 sex	MuDR	Lclav	Lc_sex	MuDR-3--DNA/MuDr_Lc	320
5.89139 sex	NONLTR	Lclav	Lc_sex	NONLTR-1--LINE/LINE_Lc	320
34.2335 sex	Penelope	Lclav	Lc_sex	Penelope-1--LINE/Penelope_Lc	320
3.30191 sex	Penelope	Lclav	Lc_sex	Penelope-2--LINE/Penelope_Lc	320
7.32359 sex	Penelope	Lclav	Lc_sex	Penelope-3--LINE/Penelope_Lc	320
10059 sex	Penelope	Lclav	Lc_sex	Penelope-4--LINE/Penelope_Lc	320
79.9436 sex	PiggyBac	Lclav	Lc_sex	PiggyBac-1--DNA/PiggyBac_Lc	320
126668 sex	PiggyBac	Lclav	Lc_sex	PiggyBac-2--DNA/PiggyBac_Lc	320
433192 sex	PiggyBac	Lclav	Lc_sex	PiggyBac-3--DNA/PiggyBac_Lc	320
35.3466 sex	Polinton	Lclav	Lc_sex	Polinton-1--DNA/Polinton_Lc	320
86.5845 sex	Polinton	Lclav	Lc_sex	Polinton-2--DNA/Polinton_Lc	320
106252 sex	Polinton	Lclav	Lc_sex	Polinton-3--DNA/Polinton_Lc	320
60.8861 sex	Polinton	Lclav	Lc_sex	Polinton-4--DNA/Polinton_Lc	320
80.1053 sex	Polinton	Lclav	Lc_sex	Polinton-5--DNA/Polinton_Lc	320
76.8078 sex	Polinton	Lclav	Lc_sex	Polinton-6--DNA/Polinton_Lc	320
126053 sex	Polinton	Lclav	Lc_sex	Polinton-7--DNA/Polinton_Lc	320
115977 sex	Polinton	Lclav	Lc_sex	Polinton-8--DNA/Polinton_Lc	320
4321.03 sex	R1	Lclav	Lc_sex	R1-1--LINE/R1_Lc	320
901881 sex	R1	Lclav	Lc_sex	R1-2--LINE/R1_Lc	320
1034.14 sex	R1	Lclav	Lc_sex	R1-3--LINE/R1_Lc	320
1617.8 sex	R1	Lclav	Lc_sex	R1-4--LINE/R1_Lc	320
1072.34 sex	R1	Lclav	Lc_sex	R1-5--LINE/R1_Lc	320
1145.71 sex	R1	Lclav	Lc_sex	R1-6--LINE/R1_Lc	320
8.84057 sex	R1	Lclav	Lc_sex	R1-7--LINE/R1_Lc	320
18.5182 sex	R1	Lclav	Lc_sex	R1-8--LINE/R1_Lc	320
10.5039 sex	RTE	Lclav	Lc_sex	RTE-1--LINE/RTE_Lc	320
7.71712 sex	RTE	Lclav	Lc_sex	RTE-2--LINE/RTE_Lc	320
3.36137 sex	RTE	Lclav	Lc_sex	RTE-3--LINE/RTE_Lc	320
197688 sex	RTE	Lclav	Lc_sex	RTE-4--LINE/RTE_Lc	320
10.1287 sex	Sola	Lclav	Lc_sex	Sola-1--DNA/Sola_Lc	320

64.6367 sex	Sola	Lclav	Lc_sex	Sola-2--DNA/Sola_Lc	320
170256 sex	Sola	Lclav	Lc_sex	Sola-3--DNA/Sola_Lc	320
736713 sex	Sola	Lclav	Lc_sex	Sola-4--DNA/Sola_Lc	320
4.54582 sex	Sola	Lclav	Lc_sex	Sola-5--DNA/Sola_Lc	320
8.95227 sex	Sola	Lclav	Lc_sex	Sola-6--DNA/Sola_Lc	320
10.5682 sex	TcMar	Lclav	Lc_sex	TcMar-1--DNA/TcMar_Lc	320
34.6852 sex	TcMar	Lclav	Lc_sex	TcMar-2--DNA/TcMar_Lc	320
933202 sex	TcMar	Lclav	Lc_sex	TcMar-3--DNA/TcMar_Lc	320
364147 sex	TcMar_Chapaev	Lclav	Lc_sex	TcMar_Chapaev-1--DNA/TcMar_Lc	320
340378 sex	Transib	Lclav	Lc_sex	Transib-1--DNA/Transib_Lc	320
1091.97 sex	Transib	Lclav	Lc_sex	Transib-2--DNA/Transib_Lc	320
11.4513 sex	CR1	Ori	Ac	CR1-1_Ac--LINE/CR1_Ac	164
105922 sex	Gypsy	Ori	Ac	Gypsy-10_Ac--LTR/Gypsy_Ac	164
42.0374 sex	Gypsy	Ori	Ac	Gypsy-11_Ac--LTR/Gypsy_Ac	164
97.4979 sex	Gypsy	Ori	Ac	Gypsy-12_Ac--LTR/Gypsy_Ac	164
51.7685 sex	Gypsy	Ori	Ac	Gypsy-13_Ac--LTR/Gypsy_Ac	164
30.2706 sex	Gypsy	Ori	Ac	Gypsy-14_Ac--LTR/Gypsy_Ac	164
30.3561 sex	Gypsy	Ori	Ac	Gypsy-15_Ac--LTR/Gypsy_Ac	164
46.1529 sex	Gypsy	Ori	Ac	Gypsy-16_Ac--LTR/Gypsy_Ac	164
185213 sex	Gypsy	Ori	Ac	Gypsy-17_Ac--LTR/Gypsy_Ac	164
17.9273 sex	Gypsy	Ori	Ac	Gypsy-18_Ac--LTR/Gypsy_Ac	164
12.9302 sex	Gypsy	Ori	Ac	Gypsy-19_Ac--LTR/Gypsy_Ac	164
52.7546 sex	Gypsy	Ori	Ac	Gypsy-1_Ac--LTR/Gypsy_Ac	164
35.9932 sex	Gypsy	Ori	Ac	Gypsy-20_Ac--LTR/Gypsy_Ac	164
64599 sex	Gypsy	Ori	Ac	Gypsy-21_Ac--LTR/Gypsy_Ac	164
29874 sex	Gypsy	Ori	Ac	Gypsy-22_Ac--LTR/Gypsy_Ac	164
43.41 sex	Gypsy	Ori	Ac	Gypsy-23_Ac--LTR/Gypsy_Ac	164
77229 sex	Gypsy	Ori	Ac	Gypsy-24_Ac--LTR/Gypsy_Ac	164
41086 sex	Gypsy	Ori	Ac	Gypsy-25_Ac--LTR/Gypsy_Ac	164
57.3514 sex	Gypsy	Ori	Ac	Gypsy-26_Ac--LTR/Gypsy_Ac	164
28.0877 sex	Gypsy	Ori	Ac	Gypsy-27_Ac--LTR/Gypsy_Ac	164
41.6482 sex	Gypsy	Ori	Ac	Gypsy-28_Ac--LTR/Gypsy_Ac	164
94.2725 sex	Gypsy	Ori	Ac	Gypsy-29_Ac--LTR/Gypsy_Ac	164
67.0589 sex	Gypsy	Ori	Ac	Gypsy-2_Ac--LTR/Gypsy_Ac	164
44.1023 sex	Gypsy	Ori	Ac	Gypsy-30_Ac--LTR/Gypsy_Ac	164
56.3293 sex	Gypsy	Ori	Ac	Gypsy-31_Ac--LTR/Gypsy_Ac	164
72.0162 sex	Gypsy	Ori	Ac	Gypsy-3_Ac--LTR/Gypsy_Ac	164
77.6869 sex	Gypsy	Ori	Ac	Gypsy-4_Ac--LTR/Gypsy_Ac	164
169866 sex	Gypsy	Ori	Ac	Gypsy-5_Ac--LTR/Gypsy_Ac	164
40.7672 sex	Gypsy	Ori	Ac	Gypsy-6_Ac--LTR/Gypsy_Ac	164
97.2394 sex	Gypsy	Ori	Ac	Gypsy-7_Ac--LTR/Gypsy_Ac	164
54.6951 sex	Gypsy	Ori	Ac	Gypsy-8_Ac--LTR/Gypsy_Ac	164
37609 sex	Gypsy	Ori	Ac	Gypsy-9_Ac--LTR/Gypsy_Ac	164
33.9205 sex	HAT	Ori	Ac	HAT-1_Ac--DNA/hAT_Ac	164
32.4575 sex	HAT	Ori	Ac	HAT-2_Ac--DNA/hAT_Ac	164
97.4653 sex	HAT	Ori	Ac	HAT-3_Ac--DNA/hAT_Ac	164
45.1906 sex	Helitron	Ori	Ac	Helitron-1_Ac--DNA/Helitron_Ac	164
49.4607 sex	Helitron	Ori	Ac	Helitron-2_Ac--DNA/Helitron_Ac	164
47.8818 sex	Helitron	Ori	Ac	Helitron-3_Ac--DNA/Helitron_Ac	164
12651 sex	L2	Ori	Ac	L2-1_Ac--LINE/L2_Ac	164
34.9948 sex	LTR	Ori	Ac	LTR-1_Ac--LTR/LTR_Ac	164
44.0056 sex	LTR	Ori	Ac	LTR-2_Ac--LTR/LTR_Ac	164
10.4512 sex	Penelope	Ori	Ac	Penelope-1_Ac--LINE/Penelope_Ac	164
33.7894 sex	Polinton	Ori	Ac	Polinton-10_Ac--DNA/Polinton_Ac	164
35062 sex	Polinton	Ori	Ac	Polinton-11_Ac--DNA/Polinton_Ac	164
35.6408 sex	Polinton	Ori	Ac	Polinton-12_Ac--DNA/Polinton_Ac	164
106238 sex	Polinton	Ori	Ac	Polinton-13_Ac--DNA/Polinton_Ac	164
41.2795 sex	Polinton	Ori	Ac	Polinton-14_Ac--DNA/Polinton_Ac	164
62.9434 sex	Polinton	Ori	Ac	Polinton-15_Ac--DNA/Polinton_Ac	164
103922 sex	Polinton	Ori	Ac	Polinton-16_Ac--DNA/Polinton_Ac	164

38.3217 sex	Polinton	Ori	Ac	Polinton-17_Ac--DNA/Polinton_Ac	164
71.7904 sex	Polinton	Ori	Ac	Polinton-18_Ac--DNA/Polinton_Ac	164
77.7115 sex	Polinton	Ori	Ac	Polinton-19_Ac--DNA/Polinton_Ac	164
97.3818 sex	Polinton	Ori	Ac	Polinton-1_Ac--DNA/Polinton_Ac	164
59.7903 sex	Polinton	Ori	Ac	Polinton-20_Ac--DNA/Polinton_Ac	164
33.1811 sex	Polinton	Ori	Ac	Polinton-21_Ac--DNA/Polinton_Ac	164
74057 sex	Polinton	Ori	Ac	Polinton-22_Ac--DNA/Polinton_Ac	164
59.9928 sex	Polinton	Ori	Ac	Polinton-23_Ac--DNA/Polinton_Ac	164
69.4989 sex	Polinton	Ori	Ac	Polinton-24_Ac--DNA/Polinton_Ac	164
33.0898 sex	Polinton	Ori	Ac	Polinton-25_Ac--DNA/Polinton_Ac	164
61.6554 sex	Polinton	Ori	Ac	Polinton-26_Ac--DNA/Polinton_Ac	164
70.1575 sex	Polinton	Ori	Ac	Polinton-27_Ac--DNA/Polinton_Ac	164
43.5224 sex	Polinton	Ori	Ac	Polinton-28_Ac--DNA/Polinton_Ac	164
56.7368 sex	Polinton	Ori	Ac	Polinton-2_Ac--DNA/Polinton_Ac	164
107953 sex	Polinton	Ori	Ac	Polinton-3_Ac--DNA/Polinton_Ac	164
93.1048 sex	Polinton	Ori	Ac	Polinton-4_Ac--DNA/Polinton_Ac	164
106073 sex	Polinton	Ori	Ac	Polinton-5_Ac--DNA/Polinton_Ac	164
41.5752 sex	Polinton	Ori	Ac	Polinton-6_Ac--DNA/Polinton_Ac	164
37.3889 sex	Polinton	Ori	Ac	Polinton-7_Ac--DNA/Polinton_Ac	164
37.2693 sex	Polinton	Ori	Ac	Polinton-8_Ac--DNA/Polinton_Ac	164
69.1458 sex	Polinton	Ori	Ac	Polinton-9_Ac--DNA/Polinton_Ac	164
173455 sex	R1	Ori	Ac	R1-1_Ac--LINE/R1_Ac	164
30.1386 sex	TcMar	Ori	Ac	TcMar-1_Ac--DNA/TcMar_Ac	164
64.2026 sex	TcMar	Ori	Ac	TcMar-2_Ac--DNA/TcMar_Ac	164
261827 sex	TcMar	Ori	Ac	TcMar-3_Ac--DNA/TcMar_Ac	164
108187 asex	CR1	Ori	Hr	CR1-10_Hr--LINE/CR1_Hr	228
175.12 asex	CR1	Ori	Hr	CR1-11_Hr--LINE/CR1_Hr	228
84952 asex	CR1	Ori	Hr	CR1-12_Hr--LINE/CR1_Hr	228
48.4118 asex	CR1	Ori	Hr	CR1-13_Hr--LINE/CR1_Hr	228
96.1555 asex	CR1	Ori	Hr	CR1-14_Hr--LINE/CR1_Hr	228
78.4535 asex	CR1	Ori	Hr	CR1-15_Hr--LINE/CR1_Hr	228
104329 asex	CR1	Ori	Hr	CR1-16_Hr--LINE/CR1_Hr	228
66.5886 asex	CR1	Ori	Hr	CR1-1_Hr--LINE/CR1_Hr	228
105881 asex	CR1	Ori	Hr	CR1-2_Hr--LINE/CR1_Hr	228
72337 asex	CR1	Ori	Hr	CR1-3_Hr--LINE/CR1_Hr	228
84.4122 asex	CR1	Ori	Hr	CR1-4_Hr--LINE/CR1_Hr	228
82.2679 asex	CR1	Ori	Hr	CR1-5_Hr--LINE/CR1_Hr	228
225844 asex	CR1	Ori	Hr	CR1-6_Hr--LINE/CR1_Hr	228
139235 asex	CR1	Ori	Hr	CR1-7_Hr--LINE/CR1_Hr	228
226695 asex	CR1	Ori	Hr	CR1-8_Hr--LINE/CR1_Hr	228
190298 asex	CR1	Ori	Hr	CR1-9_Hr--LINE/CR1_Hr	228
1572.16 asex	DNA-8N1	Ori	Hr	DNA-8N1_Hr	228
35.2042 asex	EnSpm	Ori	Hr	EnSpm-1_Hr--DNA/EnSpm_Hr	228
46557 asex	ERV	Ori	Hr	ERV-1_Hr--Other/ERV_Hr	228
133567 asex	Gypsy	Ori	Hr	Gypsy-1_Hr--LTR/Gypsy_Hr	228
97.4202 asex	Gypsy	Ori	Hr	Gypsy-2_Hr--LTR/Gypsy_Hr	228
65.2042 asex	Gypsy	Ori	Hr	Gypsy-3_Hr--LTR/Gypsy_Hr	228
26.9129 asex	HAT	Ori	Hr	HAT-1_Hr--DNA/hAT_Hr	228
91.5422 asex	HAT	Ori	Hr	HAT-2_Hr--DNA/hAT_Hr	228
59.8655 asex	HAT	Ori	Hr	HAT-3_Hr--DNA/hAT_Hr	228
92.5676 asex	HAT	Ori	Hr	HAT-4_Hr--DNA/hAT_Hr	228
68.3586 asex	HAT	Ori	Hr	HAT-5_Hr--DNA/hAT_Hr	228
7.57131 asex	HAT	Ori	Hr	HAT-6_Hr--DNA/hAT_Hr	228
27591 asex	HAT	Ori	Hr	HAT-7_Hr--DNA/hAT_Hr	228
50.8701 asex	HAT	Ori	Hr	HAT-8_Hr--DNA/hAT_Hr	228
183914 asex	Helitron	Ori	Hr	Helitron-1_Hr--DNA/Helitron_Hr	228
134417 asex	Helitron	Ori	Hr	Helitron-2_Hr--DNA/Helitron_Hr	228
120371 asex	Helitron	Ori	Hr	Helitron-3_Hr--DNA/Helitron_Hr	228
143427 asex	Helitron	Ori	Hr	Helitron-4_Hr--DNA/Helitron_Hr	228
174.57 asex	Helitron	Ori	Hr	Helitron-5_Hr--DNA/Helitron_Hr	228

128569 asex	Helitron	Ori	Hr	Helitron-6_Hr--DNA/Helitron_Hr	228
85062 asex	ISL2EU	Ori	Hr	ISL2EU-1_Hr--DNA/ISL2EU_Hr	228
228589 asex	ISL2EU	Ori	Hr	ISL2EU-2_Hr--DNA/ISL2EU_Hr	228
45.1929 asex	ISL2EU	Ori	Hr	ISL2EU-3_Hr--DNA/ISL2EU_Hr	228
17.8714 asex	ISL2EU	Ori	Hr	ISL2EU-4_Hr--DNA/ISL2EU_Hr	228
115989 asex	ISL2EU	Ori	Hr	ISL2EU-5_Hr--DNA/ISL2EU_Hr	228
57928 asex	ISL2EU	Ori	Hr	ISL2EU-6_Hr--DNA/ISL2EU_Hr	228
288079 asex	ISL2EU	Ori	Hr	ISL2EU-7_Hr--DNA/ISL2EU_Hr	228
55.2589 asex	ISL2EU	Ori	Hr	ISL2EU-8_Hr--DNA/ISL2EU_Hr	228
98.9811 asex	Merlin	Ori	Hr	Merlin-1_Hr--DNA/Merlin_Hr	228
48.3904 asex	Merlin	Ori	Hr	Merlin-2_Hr--DNA/Merlin_Hr	228
67.4989 asex	Merlin	Ori	Hr	Merlin-3_Hr--DNA/Merlin_Hr	228
41.5393 asex	MuDR	Ori	Hr	MuDR-1_Hr--DNA/MuDr_Hr	228
31.5292 asex	PiggyBac	Ori	Hr	PiggyBac-1_Hr--DNA/PiggyBac_Hr	228
81.0685 asex	Polinton	Ori	Hr	Polinton-10_Hr--DNA/Polinton_Hr	228
38.0382 asex	Polinton	Ori	Hr	Polinton-11_Hr--DNA/Polinton_Hr	228
71.9413 asex	Polinton	Ori	Hr	Polinton-12_Hr--DNA/Polinton_Hr	228
93.9229 asex	Polinton	Ori	Hr	Polinton-13_Hr--DNA/Polinton_Hr	228
134322 asex	Polinton	Ori	Hr	Polinton-14_Hr--DNA/Polinton_Hr	228
46.3592 asex	Polinton	Ori	Hr	Polinton-15_Hr--DNA/Polinton_Hr	228
70.0898 asex	Polinton	Ori	Hr	Polinton-16_Hr--DNA/Polinton_Hr	228
265899 asex	Polinton	Ori	Hr	Polinton-17_Hr--DNA/Polinton_Hr	228
106824 asex	Polinton	Ori	Hr	Polinton-18_Hr--DNA/Polinton_Hr	228
82.8521 asex	Polinton	Ori	Hr	Polinton-19_Hr--DNA/Polinton_Hr	228
73.6358 asex	Polinton	Ori	Hr	Polinton-1_Hr--DNA/Polinton_Hr	228
76.8973 asex	Polinton	Ori	Hr	Polinton-20_Hr--DNA/Polinton_Hr	228
95.27 asex	Polinton	Ori	Hr	Polinton-21_Hr--DNA/Polinton_Hr	228
33.8642 asex	Polinton	Ori	Hr	Polinton-22_Hr--DNA/Polinton_Hr	228
122597 asex	Polinton	Ori	Hr	Polinton-23_Hr--DNA/Polinton_Hr	228
75.4019 asex	Polinton	Ori	Hr	Polinton-24_Hr--DNA/Polinton_Hr	228
52.4706 asex	Polinton	Ori	Hr	Polinton-25_Hr--DNA/Polinton_Hr	228
72.7993 asex	Polinton	Ori	Hr	Polinton-26_Hr--DNA/Polinton_Hr	228
87.5725 asex	Polinton	Ori	Hr	Polinton-27_Hr--DNA/Polinton_Hr	228
94.6827 asex	Polinton	Ori	Hr	Polinton-28_Hr--DNA/Polinton_Hr	228
49.6518 asex	Polinton	Ori	Hr	Polinton-29_Hr--DNA/Polinton_Hr	228
116116 asex	Polinton	Ori	Hr	Polinton-2_Hr--DNA/Polinton_Hr	228
154.06 asex	Polinton	Ori	Hr	Polinton-30_Hr--DNA/Polinton_Hr	228
62675 asex	Polinton	Ori	Hr	Polinton-31_Hr--DNA/Polinton_Hr	228
292127 asex	Polinton	Ori	Hr	Polinton-32_Hr--DNA/Polinton_Hr	228
74.0112 asex	Polinton	Ori	Hr	Polinton-33_Hr--DNA/Polinton_Hr	228
95.2359 asex	Polinton	Ori	Hr	Polinton-34_Hr--DNA/Polinton_Hr	228
116221 asex	Polinton	Ori	Hr	Polinton-3_Hr--DNA/Polinton_Hr	228
76.5397 asex	Polinton	Ori	Hr	Polinton-4_Hr--DNA/Polinton_Hr	228
66.0838 asex	Polinton	Ori	Hr	Polinton-5_Hr--DNA/Polinton_Hr	228
95.1497 asex	Polinton	Ori	Hr	Polinton-6_Hr--DNA/Polinton_Hr	228
120677 asex	Polinton	Ori	Hr	Polinton-7_Hr--DNA/Polinton_Hr	228
38.9164 asex	Polinton	Ori	Hr	Polinton-8_Hr--DNA/Polinton_Hr	228
175432 asex	Polinton	Ori	Hr	Polinton-9_Hr--DNA/Polinton_Hr	228
34.3813 asex	R1	Ori	Hr	R1-1_Hr--LINE/R1_Hr	228
32.0611 asex	R1	Ori	Hr	R1-2_Hr--LINE/R1_Hr	228
37.4114 asex	R1	Ori	Hr	R1-3_Hr--LINE/R1_Hr	228
42.9713 asex	R1	Ori	Hr	R1-4_Hr--LINE/R1_Hr	228
25.0504 asex	TcMar	Ori	Hr	TcMar-10_Hr--DNA/TcMar_Hr	228
104058 asex	TcMar	Ori	Hr	TcMar-11_Hr--DNA/TcMar_Hr	228
27.5663 asex	TcMar	Ori	Hr	TcMar-12_Hr--DNA/TcMar_Hr	228
56.0004 asex	TcMar	Ori	Hr	TcMar-13_Hr--DNA/TcMar_Hr	228
85.2154 asex	TcMar	Ori	Hr	TcMar-14_Hr--DNA/TcMar_Hr	228
50.6362 asex	TcMar	Ori	Hr	TcMar-15_Hr--DNA/TcMar_Hr	228
126897 asex	TcMar	Ori	Hr	TcMar-16_Hr--DNA/TcMar_Hr	228
157584 asex	TcMar	Ori	Hr	TcMar-17_Hr--DNA/TcMar_Hr	228

155581 asex	TcMar	Ori	Hr	TcMar-18_Hr--DNA/TcMar_Hr	228
317481 asex	TcMar	Ori	Hr	TcMar-19_Hr--DNA/TcMar_Hr	228
37.8199 asex	TcMar	Ori	Hr	TcMar-1_Hr--DNA/TcMar_Hr	228
389.41 asex	TcMar	Ori	Hr	TcMar-20_Hr--DNA/TcMar_Hr	228
26618 asex	TcMar	Ori	Hr	TcMar-21_Hr--DNA/TcMar_Hr	228
38.4851 asex	TcMar	Ori	Hr	TcMar-22_Hr--DNA/TcMar_Hr	228
72.5976 asex	TcMar	Ori	Hr	TcMar-23_Hr--DNA/TcMar_Hr	228
31.4391 asex	TcMar	Ori	Hr	TcMar-24_Hr--DNA/TcMar_Hr	228
107367 asex	TcMar	Ori	Hr	TcMar-25_Hr--DNA/TcMar_Hr	228
245.69 asex	TcMar	Ori	Hr	TcMar-26_Hr--DNA/TcMar_Hr	228
152268 asex	TcMar	Ori	Hr	TcMar-27_Hr--DNA/TcMar_Hr	228
94.0429 asex	TcMar	Ori	Hr	TcMar-28_Hr--DNA/TcMar_Hr	228
40.1523 asex	TcMar	Ori	Hr	TcMar-29_Hr--DNA/TcMar_Hr	228
525933 asex	TcMar	Ori	Hr	TcMar-2_Hr--DNA/TcMar_Hr	228
25.0749 asex	TcMar	Ori	Hr	TcMar-30_Hr--DNA/TcMar_Hr	228
83593 asex	TcMar	Ori	Hr	TcMar-3_Hr--DNA/TcMar_Hr	228
729378 asex	TcMar	Ori	Hr	TcMar-4_Hr--DNA/TcMar_Hr	228
36.2955 asex	TcMar	Ori	Hr	TcMar-5_Hr--DNA/TcMar_Hr	228
171132 asex	TcMar	Ori	Hr	TcMar-6_Hr--DNA/TcMar_Hr	228
4222.27 asex	TcMar	Ori	Hr	TcMar-7_Hr--DNA/TcMar_Hr	228
118923 asex	TcMar	Ori	Hr	TcMar-8_Hr--DNA/TcMar_Hr	228
76.8017 asex	TcMar	Ori	Hr	TcMar-9_Hr--DNA/TcMar_Hr	228
67.3894 asex	Gypsy	Ori	Pp	Gypsy-1_Pp--LTR/Gypsy_Pp	220
5.98507 asex	HAT	Ori	Pp	HAT-1_Pp--DNA/hAT_Pp	220
375276 asex	ISL2EU	Ori	Pp	ISL2EU-1_Pp--DNA/ISL2EU_Pp	220
114721 asex	Penelope	Ori	Pp	Penelope-1_Pp--LINE/Penelope_Pp	220
261.51 asex	Polinton	Ori	Pp	Polinton-1_Pp--DNA/Polinton_Pp	220
136913 asex	Polinton	Ori	Pp	Polinton-2_Pp--DNA/Polinton_Pp	220
173711 asex	Polinton	Ori	Pp	Polinton-3_Pp--DNA/Polinton_Pp	220
185324 asex	Polinton	Ori	Pp	Polinton-4_Pp--DNA/Polinton_Pp	220
184.22 asex	Polinton	Ori	Pp	Polinton-5_Pp--DNA/Polinton_Pp	220
292926 asex	Polinton	Ori	Pp	Polinton-6_Pp--DNA/Polinton_Pp	220
256357 asex	Polinton	Ori	Pp	Polinton-7_Pp--DNA/Polinton_Pp	220
270546 asex	Polinton	Ori	Pp	Polinton-8_Pp--DNA/Polinton_Pp	220
244602 asex	Polinton	Ori	Pp	Polinton-9_Pp--DNA/Polinton_Pp	220
6.94614 asex	R1	Ori	Pp	R1-1_Pp--LINE/R1_Pp	220
2.35748 asex	R1	Ori	Pp	R1-2_Pp--LINE/R1_Pp	220
92.4131 asex	TcMar	Ori	Pp	TcMar-1_Pp--DNA/TcMar_Pp	220
8.14931 sex	DNA_transposon	Ori	Sm	DNA_transposon-1_Sm--DNA/DNA_Sm	240
13.2351 sex	DNA_transposon	Ori	Sm	DNA_transposon-2_Sm--DNA/DNA_Sm	240
11.5204 sex	DNA_transposon	Ori	Sm	DNA_transposon-3_Sm--DNA/DNA_Sm	240
4.92942 sex	Gypsy	Ori	Sm	Gypsy-10_Sm--LTR/Gypsy_Sm	240
8.44477 sex	Gypsy	Ori	Sm	Gypsy-11_Sm--LTR/Gypsy_Sm	240
25.2711 sex	Gypsy	Ori	Sm	Gypsy-12_Sm--LTR/Gypsy_Sm	240
182845 sex	Gypsy	Ori	Sm	Gypsy-13_Sm--LTR/Gypsy_Sm	240
272337 sex	Gypsy	Ori	Sm	Gypsy-14_Sm--LTR/Gypsy_Sm	240
149299 sex	Gypsy	Ori	Sm	Gypsy-15_Sm--LTR/Gypsy_Sm	240
180717 sex	Gypsy	Ori	Sm	Gypsy-16_Sm--LTR/Gypsy_Sm	240
215013 sex	Gypsy	Ori	Sm	Gypsy-17_Sm--LTR/Gypsy_Sm	240
190216 sex	Gypsy	Ori	Sm	Gypsy-1_Sm--LTR/Gypsy_Sm	240
203436 sex	Gypsy	Ori	Sm	Gypsy-2_Sm--LTR/Gypsy_Sm	240
6.20349 sex	Gypsy	Ori	Sm	Gypsy-3_Sm--LTR/Gypsy_Sm	240
167125 sex	Gypsy	Ori	Sm	Gypsy-4_Sm--LTR/Gypsy_Sm	240
236646 sex	Gypsy	Ori	Sm	Gypsy-5_Sm--LTR/Gypsy_Sm	240
14.7722 sex	Gypsy	Ori	Sm	Gypsy-6_Sm--LTR/Gypsy_Sm	240
55.6097 sex	Gypsy	Ori	Sm	Gypsy-7_Sm--LTR/Gypsy_Sm	240
213919 sex	Gypsy	Ori	Sm	Gypsy-8_Sm--LTR/Gypsy_Sm	240
154809 sex	Gypsy	Ori	Sm	Gypsy-9_Sm--LTR/Gypsy_Sm	240
12.6499 sex	HAT	Ori	Sm	HAT-1_Sm--DNA/hAT_Sm	240
139819 sex	Helitron	Ori	Sm	Helitron-10_Sm--DNA/Helitron_Sm	240

251812 sex	Helitron	Ori	Sm	Helitron-11_Sm--DNA/Helitron_Sm	240
213589 sex	Helitron	Ori	Sm	Helitron-12_Sm--DNA/Helitron_Sm	240
133155 sex	Helitron	Ori	Sm	Helitron-13_Sm--DNA/Helitron_Sm	240
190772 sex	Helitron	Ori	Sm	Helitron-14_Sm--DNA/Helitron_Sm	240
225877 sex	Helitron	Ori	Sm	Helitron-15_Sm--DNA/Helitron_Sm	240
365714 sex	Helitron	Ori	Sm	Helitron-16_Sm--DNA/Helitron_Sm	240
188145 sex	Helitron	Ori	Sm	Helitron-17_Sm--DNA/Helitron_Sm	240
355537 sex	Helitron	Ori	Sm	Helitron-18_Sm--DNA/Helitron_Sm	240
351832 sex	Helitron	Ori	Sm	Helitron-19_Sm--DNA/Helitron_Sm	240
308976 sex	Helitron	Ori	Sm	Helitron-1_Sm--DNA/Helitron_Sm	240
454071 sex	Helitron	Ori	Sm	Helitron-20_Sm--DNA/Helitron_Sm	240
408.51 sex	Helitron	Ori	Sm	Helitron-21_Sm--DNA/Helitron_Sm	240
71.2804 sex	Helitron	Ori	Sm	Helitron-22_Sm--DNA/Helitron_Sm	240
447413 sex	Helitron	Ori	Sm	Helitron-23_Sm--DNA/Helitron_Sm	240
282359 sex	Helitron	Ori	Sm	Helitron-24_Sm--DNA/Helitron_Sm	240
84.7621 sex	Helitron	Ori	Sm	Helitron-25_Sm--DNA/Helitron_Sm	240
452364 sex	Helitron	Ori	Sm	Helitron-26_Sm--DNA/Helitron_Sm	240
258664 sex	Helitron	Ori	Sm	Helitron-27_Sm--DNA/Helitron_Sm	240
432044 sex	Helitron	Ori	Sm	Helitron-28_Sm--DNA/Helitron_Sm	240
182024 sex	Helitron	Ori	Sm	Helitron-29_Sm--DNA/Helitron_Sm	240
334373 sex	Helitron	Ori	Sm	Helitron-2_Sm--DNA/Helitron_Sm	240
530274 sex	Helitron	Ori	Sm	Helitron-30_Sm--DNA/Helitron_Sm	240
315043 sex	Helitron	Ori	Sm	Helitron-31_Sm--DNA/Helitron_Sm	240
317939 sex	Helitron	Ori	Sm	Helitron-32_Sm--DNA/Helitron_Sm	240
514228 sex	Helitron	Ori	Sm	Helitron-3_Sm--DNA/Helitron_Sm	240
431877 sex	Helitron	Ori	Sm	Helitron-4_Sm--DNA/Helitron_Sm	240
320095 sex	Helitron	Ori	Sm	Helitron-5_Sm--DNA/Helitron_Sm	240
180426 sex	Helitron	Ori	Sm	Helitron-6_Sm--DNA/Helitron_Sm	240
79.7282 sex	Helitron	Ori	Sm	Helitron-7_Sm--DNA/Helitron_Sm	240
1053.2 sex	Helitron	Ori	Sm	Helitron-8_Sm--DNA/Helitron_Sm	240
31.4544 sex	Helitron	Ori	Sm	Helitron-9_Sm--DNA/Helitron_Sm	240
14.6687 sex	IS3EU	Ori	Sm	IS3EU-1_Sm--DNA/IS3EU_Sm	240
26.0146 sex	Merlin	Ori	Sm	Merlin-1_Sm--DNA/Merlin_Sm	240
14.1798 sex	MuDR	Ori	Sm	MuDR-1_Sm--DNA/MuDr_Sm	240
1076.44 sex	NONAUTONOM	Ori	Sm	NONAUTONOM-1_Sm--Other/nonautono	240
41.0582 sex	NONAUTONOM	Ori	Sm	NONAUTONOM-2_Sm--Other/nonautono	240
7.97236 sex	Penelope	Ori	Sm	Penelope-1_Sm--LINE/Penelope_Sm	240
1020.07 sex	Penelope	Ori	Sm	Penelope-2_Sm--LINE/Penelope_Sm	240
9.49089 sex	Penelope	Ori	Sm	Penelope-3_Sm--LINE/Penelope_Sm	240
10.6726 sex	Penelope	Ori	Sm	Penelope-4_Sm--LINE/Penelope_Sm	240
218312 sex	Polinton	Ori	Sm	Polinton-10_Sm--DNA/Polinton_Sm	240
268199 sex	Polinton	Ori	Sm	Polinton-11_Sm--DNA/Polinton_Sm	240
286674 sex	Polinton	Ori	Sm	Polinton-12_Sm--DNA/Polinton_Sm	240
325418 sex	Polinton	Ori	Sm	Polinton-13_Sm--DNA/Polinton_Sm	240
315871 sex	Polinton	Ori	Sm	Polinton-14_Sm--DNA/Polinton_Sm	240
149506 sex	Polinton	Ori	Sm	Polinton-15_Sm--DNA/Polinton_Sm	240
192.89 sex	Polinton	Ori	Sm	Polinton-16_Sm--DNA/Polinton_Sm	240
244082 sex	Polinton	Ori	Sm	Polinton-17_Sm--DNA/Polinton_Sm	240
374826 sex	Polinton	Ori	Sm	Polinton-18_Sm--DNA/Polinton_Sm	240
248501 sex	Polinton	Ori	Sm	Polinton-19_Sm--DNA/Polinton_Sm	240
10.4018 sex	Polinton	Ori	Sm	Polinton-1_Sm--DNA/Polinton_Sm	240
256712 sex	Polinton	Ori	Sm	Polinton-20_Sm--DNA/Polinton_Sm	240
170538 sex	Polinton	Ori	Sm	Polinton-21_Sm--DNA/Polinton_Sm	240
323456 sex	Polinton	Ori	Sm	Polinton-22_Sm--DNA/Polinton_Sm	240
112804 sex	Polinton	Ori	Sm	Polinton-23_Sm--DNA/Polinton_Sm	240
240319 sex	Polinton	Ori	Sm	Polinton-24_Sm--DNA/Polinton_Sm	240
264849 sex	Polinton	Ori	Sm	Polinton-25_Sm--DNA/Polinton_Sm	240
11.1048 sex	Polinton	Ori	Sm	Polinton-26_Sm--DNA/Polinton_Sm	240
246165 sex	Polinton	Ori	Sm	Polinton-27_Sm--DNA/Polinton_Sm	240
122697 sex	Polinton	Ori	Sm	Polinton-28_Sm--DNA/Polinton_Sm	240

144841 sex	Polinton	Ori	Sm	Polinton-29_Sm--DNA/Polinton_Sm	240
27.5524 sex	Polinton	Ori	Sm	Polinton-2_Sm--DNA/Polinton_Sm	240
83.4813 sex	Polinton	Ori	Sm	Polinton-30_Sm--DNA/Polinton_Sm	240
131069 sex	Polinton	Ori	Sm	Polinton-31_Sm--DNA/Polinton_Sm	240
204965 sex	Polinton	Ori	Sm	Polinton-32_Sm--DNA/Polinton_Sm	240
132.67 sex	Polinton	Ori	Sm	Polinton-33_Sm--DNA/Polinton_Sm	240
154217 sex	Polinton	Ori	Sm	Polinton-34_Sm--DNA/Polinton_Sm	240
99614 sex	Polinton	Ori	Sm	Polinton-35_Sm--DNA/Polinton_Sm	240
233311 sex	Polinton	Ori	Sm	Polinton-36_Sm--DNA/Polinton_Sm	240
111758 sex	Polinton	Ori	Sm	Polinton-37_Sm--DNA/Polinton_Sm	240
243.58 sex	Polinton	Ori	Sm	Polinton-38_Sm--DNA/Polinton_Sm	240
24.2965 sex	Polinton	Ori	Sm	Polinton-39_Sm--DNA/Polinton_Sm	240
128205 sex	Polinton	Ori	Sm	Polinton-3_Sm--DNA/Polinton_Sm	240
228745 sex	Polinton	Ori	Sm	Polinton-40_Sm--DNA/Polinton_Sm	240
412229 sex	Polinton	Ori	Sm	Polinton-41_Sm--DNA/Polinton_Sm	240
84.8039 sex	Polinton	Ori	Sm	Polinton-42_Sm--DNA/Polinton_Sm	240
225.71 sex	Polinton	Ori	Sm	Polinton-43_Sm--DNA/Polinton_Sm	240
259151 sex	Polinton	Ori	Sm	Polinton-44_Sm--DNA/Polinton_Sm	240
188894 sex	Polinton	Ori	Sm	Polinton-45_Sm--DNA/Polinton_Sm	240
315951 sex	Polinton	Ori	Sm	Polinton-46_Sm--DNA/Polinton_Sm	240
102054 sex	Polinton	Ori	Sm	Polinton-47_Sm--DNA/Polinton_Sm	240
237687 sex	Polinton	Ori	Sm	Polinton-48_Sm--DNA/Polinton_Sm	240
121018 sex	Polinton	Ori	Sm	Polinton-49_Sm--DNA/Polinton_Sm	240
91.9329 sex	Polinton	Ori	Sm	Polinton-4_Sm--DNA/Polinton_Sm	240
368844 sex	Polinton	Ori	Sm	Polinton-50_Sm--DNA/Polinton_Sm	240
102528 sex	Polinton	Ori	Sm	Polinton-51_Sm--DNA/Polinton_Sm	240
211535 sex	Polinton	Ori	Sm	Polinton-52_Sm--DNA/Polinton_Sm	240
138046 sex	Polinton	Ori	Sm	Polinton-53_Sm--DNA/Polinton_Sm	240
158595 sex	Polinton	Ori	Sm	Polinton-54_Sm--DNA/Polinton_Sm	240
257377 sex	Polinton	Ori	Sm	Polinton-55_Sm--DNA/Polinton_Sm	240
138732 sex	Polinton	Ori	Sm	Polinton-56_Sm--DNA/Polinton_Sm	240
125516 sex	Polinton	Ori	Sm	Polinton-57_Sm--DNA/Polinton_Sm	240
120823 sex	Polinton	Ori	Sm	Polinton-58_Sm--DNA/Polinton_Sm	240
277598 sex	Polinton	Ori	Sm	Polinton-59_Sm--DNA/Polinton_Sm	240
101254 sex	Polinton	Ori	Sm	Polinton-5_Sm--DNA/Polinton_Sm	240
258689 sex	Polinton	Ori	Sm	Polinton-60_Sm--DNA/Polinton_Sm	240
137.93 sex	Polinton	Ori	Sm	Polinton-61_Sm--DNA/Polinton_Sm	240
113147 sex	Polinton	Ori	Sm	Polinton-62_Sm--DNA/Polinton_Sm	240
236222 sex	Polinton	Ori	Sm	Polinton-63_Sm--DNA/Polinton_Sm	240
90.2855 sex	Polinton	Ori	Sm	Polinton-64_Sm--DNA/Polinton_Sm	240
160256 sex	Polinton	Ori	Sm	Polinton-65_Sm--DNA/Polinton_Sm	240
335817 sex	Polinton	Ori	Sm	Polinton-66_Sm--DNA/Polinton_Sm	240
364.27 sex	Polinton	Ori	Sm	Polinton-67_Sm--DNA/Polinton_Sm	240
211744 sex	Polinton	Ori	Sm	Polinton-68_Sm--DNA/Polinton_Sm	240
72.83 sex	Polinton	Ori	Sm	Polinton-69_Sm--DNA/Polinton_Sm	240
318908 sex	Polinton	Ori	Sm	Polinton-6_Sm--DNA/Polinton_Sm	240
119104 sex	Polinton	Ori	Sm	Polinton-70_Sm--DNA/Polinton_Sm	240
103275 sex	Polinton	Ori	Sm	Polinton-71_Sm--DNA/Polinton_Sm	240
110175 sex	Polinton	Ori	Sm	Polinton-72_Sm--DNA/Polinton_Sm	240
162183 sex	Polinton	Ori	Sm	Polinton-73_Sm--DNA/Polinton_Sm	240
97.4148 sex	Polinton	Ori	Sm	Polinton-74_Sm--DNA/Polinton_Sm	240
213852 sex	Polinton	Ori	Sm	Polinton-75_Sm--DNA/Polinton_Sm	240
247386 sex	Polinton	Ori	Sm	Polinton-76_Sm--DNA/Polinton_Sm	240
119198 sex	Polinton	Ori	Sm	Polinton-77_Sm--DNA/Polinton_Sm	240
251001 sex	Polinton	Ori	Sm	Polinton-78_Sm--DNA/Polinton_Sm	240
107691 sex	Polinton	Ori	Sm	Polinton-7_Sm--DNA/Polinton_Sm	240
141761 sex	Polinton	Ori	Sm	Polinton-8_Sm--DNA/Polinton_Sm	240
117193 sex	Polinton	Ori	Sm	Polinton-9_Sm--DNA/Polinton_Sm	240
8.25194 sex	R1	Ori	Sm	R1-1_Sm--LINE/R1_Sm	240
688553 sex	RTE	Ori	Sm	RTE-1_Sm--LINE/RTE_Sm	240

599659 sex	RTE	Ori	Sm	RTE-2_Sm--LINE/RTE_Sm	240
14.0717 sex	TcMar	Ori	Sm	TcMar-10_Sm--DNA/TcMar_Sm	240
43.6915 sex	TcMar	Ori	Sm	TcMar-1_Sm--DNA/TcMar_Sm	240
15.7189 sex	TcMar	Ori	Sm	TcMar-2_Sm--DNA/TcMar_Sm	240
57.5501 sex	TcMar	Ori	Sm	TcMar-3_Sm--DNA/TcMar_Sm	240
12.9092 sex	TcMar	Ori	Sm	TcMar-4_Sm--DNA/TcMar_Sm	240
84.6805 sex	TcMar	Ori	Sm	TcMar-5_Sm--DNA/TcMar_Sm	240
15.6565 sex	TcMar	Ori	Sm	TcMar-6_Sm--DNA/TcMar_Sm	240
26.6216 sex	TcMar	Ori	Sm	TcMar-7_Sm--DNA/TcMar_Sm	240
17042 sex	TcMar	Ori	Sm	TcMar-8_Sm--DNA/TcMar_Sm	240
20.3082 sex	TcMar	Ori	Sm	TcMar-9_Sm--DNA/TcMar_Sm	240